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THE DISTRIBUTION OF FREE-LIVING NEMATODES IN RELATION TO SALINITY IN THE MIDDLE AND UPPER REACHES OF THE RIVER BLYTH ESTUARY

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(With 4 Figures in the Text)

The habitat of mud-dwelling estuarine nematodes consists essentially of an extremely complex mixture (Baver 1948) of inorganic and organic particles surrounded by interstitial water. Except when the mud dries out completely the body surface of a nematode in this habitat is continually in contact with the interstitial water. Exposure, salinity changes, and other characteristics of estuaries affect nematodes only in so far as they affect conditions in this water. The ecological factors peculiar to this habitat can be seen to be very different from those affecting nematodes living on rocky shores, intertidal seaweeds or marine beaches.

The original work on the marine nematodes of this country is that of Bastian (1865). This was followed by a number of recordings and descriptions of new species made by Southern (1914) during the Clare Island survey. Since then the nematodes of the Plymouth area have been described by Schuurmans-Stekhoven (1935b) and by Wieser (1951, 1952) in two important works. In his latest paper Wieser studied the vertical distribution of nematodes inhabiting intertidal seaweeds, and although the detailed ecology of the species found in this habitat cannot be extrapolated to the present investigation, the species recordings and the general intertidal ecology of the nematodes studied have been useful for comparison. Moore (1931) and Mare (1942) have studied nematodes as a group, without distinguishing the species, during wider investigations on marine benthic communities, and Rees (1940) has dealt generally with intertidal nematodes. The work of Rees dealt with the horizontal and vertical distribution of nematodes found during a wider survey of the ecology of a mud flat in the Bristol Channel, but none was identified. His work has been used as the only available point of departure for the present investigation.

The distribution of free-living nematodes in water of varying salinity has been the subject of much research in the Baltic and in certain areas of the Zuiderzee. An extensive literature exists for the Belgian coast, the North Sea coast of Germany and the Dutch coast, which is summarized in Schuurmans-Stekhoven (1935a) and more recently by Wieser (1951). In the Zuiderzee and the Baltic, rates of salinity change are much less rapid than those found in estuaries and the distribution of

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nematodes under conditions of high rates of change has not previously been studied.

Rees (1940) has shown that nematodes inhabiting intertidal mud have their largest population densities in the surface 1 cm, and that as depth increases population densities decrease until at a depth of 5 cm few nematodes are found. It has not been possible to study variation in interstitial salinities with depth, but an account of variations in the top 2 cm has been given (Capstick 1957). In this paper the whole of the nematode population in the surface 5 cm of mud has been grouped without regard to its vertical distribution.

The River Blyth estuary is 3·8 miles long; the middle and upper reaches are almost emptied of tidal water at LWS exposing extensive areas of intertidal mud.

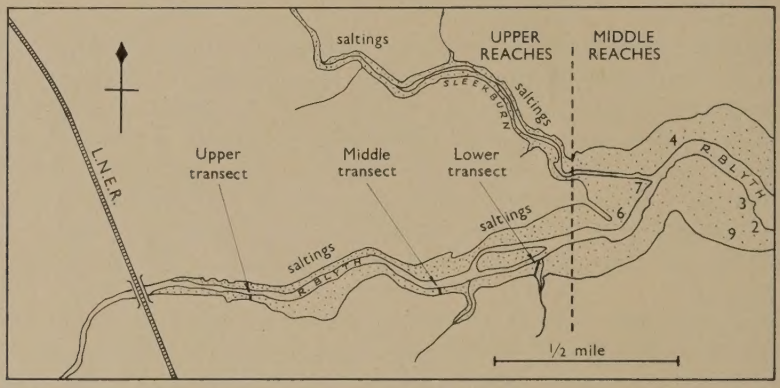

Fig. 1. The middle and upper reaches of the Blyth estuary showing the positions of the sampling stations in the middle reaches (numbers) and of the transects in the upper reaches. Areas of mud stippled.

The salinity characteristics of the tidal and the interstitial water of the estuarine muds have been described in a previous paper (Capstick 1957).

METHODS

Samples of mud from the estuary were first taken with a piece of iron piping of 3·3 cm internal diameter and a wooden plunger or ramrod. This method was inconvenient because a number of screw-topped jars had to be carried on to soft mud to hold the samples. Only the samples for Stations 2, 3, 4, 6 and 7 (Middle Reaches, Fig. 1) were obtained by this method. Modified screw-topped aluminium containers were used to take the remaining samples. These were of 4·3 cm internal diameter, 9 cm high and 14·5 cm^2 in cross section. The bottom of each tube was removed and the cut surface smoothed and sharpened to a cutting edge. A spare top was forced on to the sharpened edge of the cylinder and the distance from the cutting edge was marked in centimetres on the outside. As combined core samplers and containers they were found to be light, strong and sufficiently watertight. In the field, both lids were removed and the tubes were forced vertically into the mud to the required depth of 5 cm. A hole was dug to one side of the tube and a trowel slid horizontally across the bottom edge, the tube containing the core was lifted and

lids were fitted to both ends. The cores were uniform and, except where gravel or stones were present, contained no air spaces.

Moore (1931), Mare (1942), Rees (1940) and Krogh & Spärck (1936) found that both marine benthic and intertidal nematode populations were largest in the surface 1-2 cm of the substratum. Below this level the population decreased steadily, until at 4-5 cm few or no nematodes were found. As the sampling tubes used in the upper reaches were all of the same diameter, differences in the size of the samples taken would be due to variations in the length of the cores. Owing to the small numbers of nematodes at the deeper levels small variations in the size of samples taken would consequently have little effect on the number of nematodes found.

At the fauna sampling stations in the middle reaches and on the lower, middle and upper transects (Fig. 1) one or more samples were taken as described below. These were used for analyses of the total nematode populations, and great care was taken to ensure that they were perfectly uniform. Compared with many species found in the estuary, *Enoplus brevis* Bastian was found to have a relatively low population density, and it was necessary to take more than one sample for an estimate of its distribution; five samples were taken at each sampling area on each of the three transects in the upper reaches. There are fourteen sampling areas of 6×20 ft on the lower transect, and nine areas of 6×10 ft on the middle and upper transects. These were contiguous, running from high to low water on each of the transects, which were established at different distances from the head of the estuary. Cross sections of each of the transects are given in a previous paper (Capstick 1957, Fig. 2, p. 299). The five tubes were thrown in a batch into each sampling area, and samples were taken where they fell. All samples examined for *E. brevis* and total nematode populations were collected from the transects between 9 and 11 April 1951. Samples were shaken from the tubes into screw-topped jars in the field, the tubes and lids were rinsed with a jet of sea water, and the washings together with 30 ml of 40% formaldehyde were added to the contents of the jar.

Two separate techniques were necessary in the examination of the samples, one for the counting of *E. brevis* and another for the estimations of the total nematode population. The former involved the extraction of a species which measures 4·6-5·4 mm in the adult stage. The object of the other technique was to retain all individuals of all species ranging in size from $<$ 1 mm to 7 mm. In both cases a sieve was used to clear the mud from the samples, and in practice some nematodes of small size were always lost with the mud. Attempts to separate nematodes from mud by density separation and modified Baermann funnels were unsatisfactory. Both the methods described here are based on the principles outlined by Cobb (1918) and Filipjev & Schuurmans-Stekhoven (1941), with sieve sizes and settling times adjusted to deal with the much larger marine nematodes which were encountered.

(*a*) *The method for* Enoplus brevis

Samples were suspended in sea water and poured on to a 30 mesh/in. sieve; the

material passing the sieve was re-sieved another three times. The sieve was inclined, and suspended material was poured directly on to the gauze and not allowed to fall on it from a height greater than 5 cm. This procedure permits more effective retention of nematodes on the gauze, because a stream of water meeting the sieve at a more perpendicular angle would have the tendency to force the nematodes through the mesh openings (Tarjan, Simanton & Russell 1956). Re-sieving the filtrate reduces the chances of loss through individuals arriving head on to the sieve apertures, particularly as nematodes are more or less tubular in shape. A 30 mesh/in. sieve allowed the maximum amount of suspended matter to pass with a minimum loss of *E. brevis* larvae but examination of the residues showed that adults did not pass the sieve. The material remaining on the sieve was washed into an enamel basin and stones and gravel removed by decantation. The suspension of nematodes was transferred to a 500 ml measuring cylinder and shaken with 400 ml of sea water, then allowed to stand for 4 sec. Water and suspended animals were decanted on to the sieve while sand remained in the cylinder. Water passing the sieve was returned to the cylinder and the decantation was repeated three times. Examination of the sand left after decantation failed to reveal any nematodes. Material retained on the sieve was washed off and searched twice in a counting chamber using a binocular dissecting microscope. All nematodes resembling *E. brevis* were picked out and examined in a polyvinyl alcohol mounting medium (Gray & Wess 1950) at higher magnifications. Nematodes identified as *E. brevis* were classified as males, females or larvae.

(*b*) *The method for total nematode populations*

This method was designed to retain the maximum numbers of all species for counting and identification. The numbers encountered in samples of 14·5 $cm^2 \times 5$ cm high were so large that subsampling at some stage was a necessity. The suspended sample was poured on to an inclined 60 mesh/in. sieve and the material passing the sieve was passed through a further three times. Experiments with sieves of smaller aperture proved impracticable as so much mud and sand remained that many nematodes were overlooked in the counting chamber. The sieve was then inverted and the contents washed into a 500 ml measuring cylinder for decantation. The level was adjusted to the 450 ml mark with sea water, giving a column of water 26 cm high. This was shaken and allowed to stand for 10-20 sec, depending on the amount of sand in the sample, and then decanted on to the sieve. Water passing the sieve was returned to the cylinder and the decantation repeated three times, using the same water each time. The average rate of fall in a column of sea water of adults of *E. brevis*, which was one of the largest species encountered, was found by experiment, and settling times for decantation were based on the results. It was calculated that using the maximum permitted settling time of 20 sec, only 3·4% of *E. brevis* would remain in the sediment after four decantations. Most species dealt with by this method are smaller and have a much slower rate of fall than *E. brevis*, and consequently examination of the

sediment by direct searching showed that the numbers remaining were less than 1% of the total in the sample.

At this stage the sample was ready for subsampling. A rough estimate of the number of nematodes was made, so that each subsample of 30 ml would contain approximately fifty nematodes. The subsampler (Fig. 2) was moved up and down in the measuring cylinder containing the suspended sample until it was evenly mixed. Most samples were suspended in 500 ml of sea water but this figure was

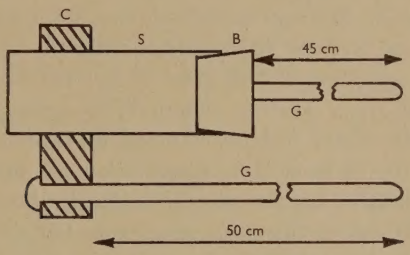

Fig. 2. The subsampler. S, glass specimen tube of 30 ml capacity; B, rubber bung; C, large cork chive; G, glass rod.

varied between 300 and 800 ml depending on the numbers of nematodes estimated to be in the sample. When the sample was evenly mixed the sampler was brought to rest in the middle of the column, the rubber bung was withdrawn, and the 30 ml subsample withdrawn immediately. In most cases two subsamples were taken each accounting for about 5% of the total volume. Each subsample was searched twice in a counting chamber and all nematodes were removed for identification.

Table 1. *The numbers of nematodes yielded by five replicate samples, when extracted and counted using the method described for total nematode populations*

Sample number	Number of nematodes in 6/50 sample	Calculated number per sample (14·5 $cm^2 \times 5$ cm)
1	94	780
2	97	810
3	83	690
4	78	650
5	87	720

If the numbers found in the two subsamples exceeded 100, the remainder of the sample was discarded; if not, another subsample was taken.

As a guide to the accuracy of this method five samples were taken within 900 cm^2 of a uniform area of mud and counted and processed as described. The samples were assumed to contain equal numbers of nematodes before processing. The results are given in Table 1 and it was found that the mean of the numbers per 6/50 sample was 87·8 with an estimated variance of 60·7. As the estimated

variance was based on only five samples it could be wide of the true value. In the case of a normal parent population, estimates of variance would fluctuate about the true value σ^2 with variance $2\sigma^4/n-1$. Where $n = 5$, the standard deviation of the estimated variance is $\sigma^2/\sqrt{2}$, which is almost as great as σ itself. The distribution of the estimated variance for $n = 5$ is skew with its mode at half the mean. In view of the possibility that the estimated variance of 60·7 could be far from the mark, this result has been tested against a simple hypothesis of randomness. This would imply a variance of 87·8, for the variance of a Poisson distribution is best estimated from its mean. The null hypothesis that the variance is 87·8 leads to a comparison of 60·7 and 87·8 by the variance ratio (F) test with 4 and infinite degrees of freedom respectively. This gives $F = 1{\cdot}445$ which is of considerably lower significance than 20%. There is, therefore, no significant difference between the estimated variance of 60·7 which was found by experiment and the mean of 87·8 which would be the variance if the distribution was of the Poisson type.

Now we wish to compare samples corresponding to identical areas, but which have different proportions of this area examined. On the hypothesis that the population densities in two sample areas (each of 14·5 cm²) were the same, we would expect the counts to be in the ratio of the percentages examined. Now it can be shown (Przyborowski & Wilenski 1940) that if the counts in two Poissonian samples, whose means are in the ratio $1 : \lambda$, are n_1 and n_2, then if the sum of the counts is $N = n_1+n_2$, n_1 is binomially distributed with mean N_p and variance N_{pq} where $p = \dfrac{1}{1+\lambda}$ and $q = \dfrac{\lambda}{1+\lambda}$.

As the numbers in the counts are large we can approximate the binomial to the normal distribution so that we may take $\dfrac{n_1-N_p}{\sqrt{N_{pq}}}$ to be a standard normal deviate with mean zero and standard deviation equal to unity, to which the normal tests apply. To facilitate the comparisons which may be required in Table 8 the 95% confidence limits for the more frequently occurring ratios ($\lambda = 1, \frac{2}{3}, \frac{1}{2}, \frac{1}{3}$) have been computed. These are so nearly linear over the range necessary for this paper that they can be represented by the following equations:

$\lambda = 1$	upper 95% confidence limits	n_1	$= 0{\cdot}53N+7{\cdot}0$
	lower ,, ,, ,,	n_1	$= 0{\cdot}47N-7{\cdot}0$
$\lambda = \frac{2}{3}$	upper ,, ,, ,,	n_1	$= 0{\cdot}63N+7{\cdot}0$
	lower ,, ,, ,,	n_1	$= 0{\cdot}57N-7{\cdot}0$
$\lambda = \frac{1}{2}$	upper ,, ,, ,,	n_1	$= 0{\cdot}695N+6{\cdot}5$
	lower ,, ,, ,,	n_1	$= 0{\cdot}64N-6{\cdot}5$
$\lambda = \frac{1}{3}$	upper ,, ,, ,,	n_1	$= 0{\cdot}78N+5{\cdot}0$
	lower ,, ,, ,,	n_1	$= 0{\cdot}72N-5{\cdot}0$

where $\lambda = \frac{\text{smallest percentage examined}}{\text{largest percentage examined}}$
and n_1 = count from largest percentage
n_2 = count from smallest percentage
and $N = n_1 + n_2$

For example, the significance of the difference between the two counts from 4·8 ft and 4·3 ft above A C D on the lower transect (the box in Table 6) can be tested as follows:

$n_1 = 155$ from 10% of the sample
$n_2 = 132$ from 5% of the sample
$N = 287$, $\lambda = \frac{5\%}{10\%} = \frac{1}{2}$.

Substituting in the equations for $\lambda = \frac{1}{2}$,
upper 95% confidence limits of $n_1 = 0{\cdot}695\ (287) + 6{\cdot}5 = 205{\cdot}5$;
lower 95% confidence limits of $n_1 = 0{\cdot}64\ (287) - 6{\cdot}5 = 176{\cdot}5$.

As the observed count of 155 lies outside of these limits the two counts are different at the 5% level of significance. By this method the reader can test the significance of sample counts from any transect or any tidal level in which he is interested. Space forbids the comparison of all sets of two counts drawn from thirty-two counts.

All nematodes were identified in polyvinyl alcohol mounting medium, and the state of maturity and sex of each individual was recorded. This information is not given in this paper, but can be obtained from the author if required. There was, however, always a small percentage of damaged specimens and small larvae which it was impossible to identify with certainty. These were recorded as unidentified. If the identification of a species was in any way doubtful, a question mark has been inserted after its specific name in the tables. In view of the time and labour involved, no attempt was made to differentiate between the species of the genus *Sabateria* and certain species of the genus *Theristus*. All identification and nomenclature is from Schuurmans-Stekhoven (1935a).

NEMATODE POPULATIONS IN THE MIDDLE REACHES OF THE ESTUARY

Generally speaking salinity conditions in the middle reaches have been shown to be more stable and marine in character than those in the upper reaches (Capstick 1957), so that in the middle reaches large differences in the composition and size of the nematode populations are more likely to be due to habitat factors other than salinity, especially as the habitats studied were deliberately chosen to range from sand at one extreme to thick black mud at the other. The positions of these sampling stations are shown in Fig. 1, while Table 2 presents estimates of the population densities of individual species and of the nematode population as a whole. *Monoposthia costata* was found at all stations and appears to be characteristic of the middle reaches and the more marine salinity conditions found there.

Although not necessarily the most abundant species at each station, population densities were much greater than those recorded in the upper reaches, *i.e.* < 140

Table 2. *Presence and absence data and population densities per 100 cm² for six stations in the middle reaches*

	Stations					
	3	2	7	9	4	6
Adoncholaimus fuscus	180	–	–	270	–	–
Anaplostoma viviparum	–	–	730	6340	+	–
Theristus acer	–	–	240	–	–	–
Odontophora armata	85	2120	2860	270	+	+
Sphaerolaimus hirsutis	–	–	–	270	–	–
Ascolaimus elongatus	145	1760	720	–	–	–
Spirina parasitifera	350	–	4760	7140	+	–
Enoplus brevis	60	–	–	635	–	–
Monoposthia costata	620	1180	5980	2530	+	+
Halichoanolaimus robustus	205	710	–	–	–	+
Trefusia longicauda	60	470	–	85	–	–
Tripyloides marinus	145	470	–	–	–	–
Sabateria spp.	30	–	3350	5060	+	–
Oxystomatina elongata	30	–	–	185	–	–
Thalassoalaimus tardus	–	–	–	–	–	+
Viscosia viscosia	60	120	–	–	–	–
Hypodontolaimus bütschlii	–	–	–	1090	–	–
H. inaequalis	–	–	–	270	–	–
Unidentified species A	795	3890	–	905	+	+
Unidentified	235	1280	2860	3250	–	–
Totals	3000	12 000	21 500	28 300	–	–
Area sampled (cm²)	16·5	8·35	8·35	14·5		
Depth of sample (cm)	0-5	0-5	0-5	0-5		
Number of samples taken	2	1	1	1		
Number of subsamples taken	4	2	2	4		
Percentage of material examined	20	10	5	7·5		
Number of nematodes examined	102	102	90	313		
Estimated number of nematodes per sample	250	1000	1800	4100		

Table 3. *The apparent relation between the total population densities in the middle reaches and the amount of mud in the substratum*

Station number	Population per 100 cm²	Common species	Type of substratum
3	3000	Sp. A (unidentified) *Monoposthia costata*	Sand
2	13 200	Sp. A *Odontophora armata*	Muddy sand with some clay and coal dust
7	23 500	*Monoposthia costata* *Spirina parasitifera*	Black mud with shells and small stones
9	28 300	*Spirina parasitifera* *Anaplostoma viviparum* *Sabateria* spp.	Thick black mud

per 100 cm² on the lower transect and < 70 per 100 cm² on the middle transect, as against 620, 1180, 5970 and 2530 per 100 cm² at stations 3, 2, 7 and 9.

When the total population densities are arranged in order of magnitude, there

appears to be some relation between the amount of mud in the substratum and the population density (Table 3). This confirms the conclusions of Schuurmans-Stekhoven, Adam & Coninck (1933) that: '. . . in general . . . the number of nematodes per c.c. of sample depends on the quantity of mud the sample contains. This seems to be contradictory to what other authors, for instance Allgen, claim. He and others are of the opinion that pure shell sand offers the best opportunities for a wealthy [*sic*] Nemic population'. In Table 3 the common species at each station are arranged in order of abundance, and it is clear that each type of substratum supports its own particular type of fauna. The quality of the substratum

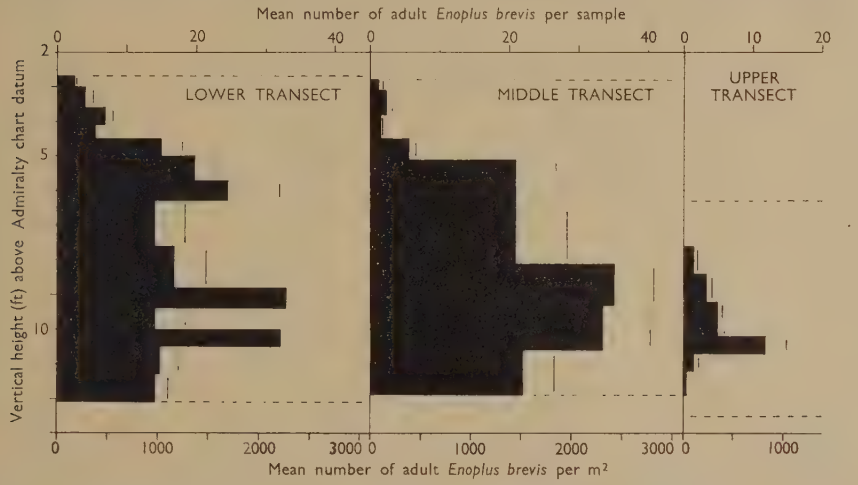

Fig. 3. The intertidal distribution of adult *Enoplus brevis* on the three transects. Each column in the histogram is the mean of five observations; the interval between the vertical line and each column represents one standard error of the mean. Horizontal broken lines show the upper and lower limits of the transects.

at station 9 was very similar to that of the lower and middle transects in the upper reaches, at both of which *Spirina parasitifera*, *Anaplostoma viviparum* and *Sabateria* spp. were the most abundant species.

THE DISTRIBUTION OF NEMATODES IN THE UPPER REACHES OF THE ESTUARY

(*a*) Enoplus brevis *Bastian*

E. brevis is larger than the majority of nematode species found in the upper reaches of the estuary, and it has a much lower population density. Because it is relatively large, easy to identify and the numbers of adults in a sample are such that subsampling is unnecessary, it has been studied in more detail than the remainder of the nematode species. The intertidal distribution of *E. brevis* has been investigated on three transects established at different positions in the upper reaches as shown in Fig. 1. Profile sections of the transects showing variations in

slope, substratum and flora, are given by Capstick (1957, Fig. 2, p. 299), but the upper and lower limits of the transects and the height of the sampling areas above Admiralty chart datum (A C D) can be seen in Fig. 3, which records the intertidal distribution as found at 9-11 April 1951.

Each of the intertidal distributions is similar in general pattern, starting with a low population density at the lowest intertidal levels nearest the edge of the river channel, rising to a maximum between 7 and 10·5 ft above A C D and then decreasing towards the upper limits of the transects. On the lower and middle transects the decrease in population density might have been more clearly demonstrated had the transects been extended a little higher, but this would have involved sampling difficulties, as the substratum at higher levels consisted mainly of gravel. In any case, the population of a primarily marine species would be expected to decrease during the transition from a marine to a terrestrial habitat. There would appear to be little difference between the recorded distributions on the lower and middle transects, although the distribution on the lower transect could be considered more variable. This may be due to the fact that there were fourteen sampling areas on the lower transect, which was 240 ft long, as against nine on the middle transect, which was 90 ft long. As the slope of the lower transect was less steep than the middle and upper transects, there is the possibility that the results were affected more by factors related to horizontal position along the length of the transect, rather than vertical position in relation to A C D.

The most striking feature of Fig. 3 is the difference between the distributions of *E. brevis* on the middle and upper transects. Although the distribution pattern on the upper transect is very similar to those of the lower and middle transects, the population densities are much smaller, and although the upper transect covers a smaller vertical distance, *E. brevis* is absent from the top and bottom ends of the transect. It would appear, therefore, that the intertidal distribution of *E. brevis* is limited at the upper and lower extremes of the transects, that this limitation becomes more severe as the head of the estuary is approached, and that overall population densities are also reduced towards the head of the estuary.

By deliberately disregarding the position of the samples in relation to A C D, it is possible to compare the average number of adults per sample found on each transect. The differences between the mean number of adults per sample on each transect, and the variance of the populations on each transect show (Table 4) that the variance of the population on the upper transect is different from that of the populations on the lower and middle transects at a significance level of 0·1 %, but that there is no difference between variances on the middle and lower transects at the 5 % level of significance. This being so, it is not permissible to compare the mean number of adults per sample on the middle and upper transects and the lower and upper transects by the use of Student's '*t*' test. However, it is obvious that the variances cannot be drawn from the same parent population, and it is a reasonable assumption that, provided the 95 % confidence limits of the means in question do not overlap, then the means are different at the 5 % level of significance, and Table 5 gives a comparison of means based on this method. It is clear

that the 95% confidence limits of the means for the lower and middle transects do overlap and therefore cannot be considered different, but that the mean for the upper transect is significantly different from the means of the middle and lower transects. Thus the average population density of *E. brevis* falls towards the head of the estuary and the largest reduction occurs between the middle and upper transect.

(*b*) *Nematode populations as a whole*

The results of the population analyses on the samples taken from the three transects are given in Tables 6 and 7. The data suggest that the total population

Table 4. *Comparison of the variance of the number of adult* Enoplus brevis *per sample on the three transects*

Transect	Variances compared	*'F'*	Degrees of freedom	Significance level
Lower Middle	198·8 273·3	0·174	69 44	< 5%
Lower Upper	198·8 20·1	5·62	69 44	> 0·1%
Middle Upper	273·3 20·1	5·20	44 44	> 0·1%

densities show a bimodal distribution on each of the transects, but it would be unwise to regard this as anything more than a suggestion for a future line of research. A much larger number of samples taken within a statistical framework would be needed to decide whether this is a true representation of the intertidal distribution of the whole nematode population, and the amount of work involved

Table 5. *Comparison of the mean number of adult* Enoplus brevis *per sample on the three transects*

Transect	Mean number of adults/sample	95% confidence limits of the mean
Lower	15·386	18·734 12·038
Middle	15·888	20·758 11·018
Upper	3·177	4·499 1·855

would (for one man) preclude the identification of individual species. Comparing transects, it is apparent that there is little difference between the total population densities on the lower and middle transects, but that those on the upper transect are much smaller than those on the middle or the lower transect. There is, moreover, little doubt that this difference is significant at the 5% level of probability. It will be remembered that this was also found to be the case for *Enoplus brevis*.

On the lower transect *Spirina parasitifera*, *Sabateria* spp., *Anaplostoma viviparum* and *Hypodontolaimus zosterae*(?) have continuous distributions along the complete

Table 6. *The intertidal distribution of the nematode populations on the lower transect*

Population densities per 100 cm²

	Height of samples (ft) above Admiralty chart datum													
	11·7	10·9	10·2	9·7	9·1	8·2	6·9	6·0	5·3	4·8	4·3	3·8	3·2	2·85
Spirina parasitifera	1170	4220	9550	4200	6660	4760	4850	5580	730	2140	2620	3930	775	910
Sabateria spp.	760	1170	2340	2290	4550	1860	2080	2910	1940	3580	6770	1790	2100	4550
Anaplostoma viviparum	2760	3040	7050	3310	2900	2210	1650	2680	1010	480	2080	895	665	2040
Hypodontolaimus bütschlii	140	415	415	140	1250	900	1030	140	135	140	135	–		–
Odontophora armata	–	275	130	70	550	70	135	480	270	480	1110	485	280	380
Enoplus brevis	350	210	275	–	405	485	475	–	370	70	135	205	–	75
Hypodontolaimus zosterae (?)	1650	550	965	1310	825	550	755	550	780	1940	3020	415	775	1290
Thalassoalaimus tardus	70	–	–	70	–	–	–	–	–	340	135	485	110	–
Adoncholaimus fuscus	70	–	–	–	65	–	–	–	–	140	–	205	–	–
Sphaerolaimus balticus	–	–	–	–	–	–	70	70	–	70	–			
S. hirsutis	–	–	–	–	–	–	–	–	50	–	–	–	–	–
Oxystomatina elongata	–	–	–	70	65	–	135	140	95	70	135	70	55	75
Paralinhomoeus lepturus	–	70	275	140	265	275	–	70	185	–	135	205	330	530
Metachromadora vivipara	–	140	–	210	135	70	–	140	–	–	–	–	–	–
Axonolaimus paraspinosus	70	140	275	–	–	140	70	70	–	–	–	135	–	–
Monoposthia costata	–	–	–	70	65	140	70	–	–	–	–	–	–	–
Theristus setosus	–	–	–	–	200	70	–	–	50	–			–	–
T. tenuispiculum	140	–	–	–	–	–	–	–	–	–	–	–	–	–
T. acer	70	–	–	–	–	–	–	–	–	–	–	–	–	–
Halichoanolaimus robustus	–	–	–	–	–	–	–	–	–	–	135	–	–	–
Oxystomatina unguiculata	–	–	–	–	–	140	–	–	–	–	–	70	–	75
Microlaimus tenuispiculum	–	–	–	–	–	–	–	–	135	70	–	–	330	–
Paracanthonchus caecus	–	–	–	–	–	–	–	–	–	–	–	–	–	75
Eutelolaimus elegans	–	–	–	–	–	–	–	–	–	–	–	–	–	75
Bathylaimus filicaudatus	–	–	–	–	–	–	–	–	–	–	–	–	–	75
Unidentified	1100	970	825	620	825	830	1580	1230	1100	1180	1790	1510	830	1350
Totals	8350	11 200	22 100	12 500	18 750	12 500	12 900	14 060	6850	10 700	18 200	10 400	6250	11 500
Area sampled (cm²)	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5	14·5
Depth of sample (cm)	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Number of subsamples taken	2	2	1	2	2	2	2	2	3	2	1	2	2	1
Per cent of material examined	10	10	5	10	10	10	10	10	15	10	5	10	12·5	9
No. of nematodes examined	121	162	160	181	272	181	187	204	149	155	132	151	113	152
Estimated number of nematodes per sample	1210	1620	3200	1810	2720	1810	1870	2040	990	1550	2640	1510	900	1690

length of the transect, while the distributions of *Hypodontolaimus bütschlii* and *Odontophora armata* show a sufficient number of records to be worth discussion. *Spirina parasitifera* reaches its maximum population density at 10·2 ft above A C D; above this level densities fall rapidly, while below they fall less rapidly and with greater variability towards the lower end of the transect. The intertidal distribution of *Anaplostoma viviparum* and *Hypodontolaimus bütschlii* follows a similar pattern, the former with less variability during the fall from the maximum to the lower end of the transect, and the latter with much lower overall population densities. The group *Sabateria* spp. has a more irregular distribution but, in general, it is the reverse of that shown by *Anaplostoma viviparum* and *Spirina parasitifera* with a maximum at 4·3 ft above A C D and a slow irregular decrease to the upper end of the transect. The intertidal distributions of *Hypodontolaimus zosterae*(?) and *Odontophora armata* follow a similar pattern, but the densities are much lower.

On the middle transect *Sabateria* spp., *Anaplostoma viviparum* and *Theristus* spp., have a continuous distribution, while *Spirina parasitifera*, *Hypodontolaimus zosterae* and *Paralinhomoeus lepturus*, although not recorded at one or two tidal levels, have interesting intertidal distributions. As on the lower transect *Spirina parasitifera* and *Anaplostoma viviparum* exhibit maximum population densities in the upper half of the transect with a gradual decrease to the upper and lower ends. The distribution of *Paralinhomoeus lepturus* is similar but densities are much lower. Once again *Sabateria* spp. show the opposite tendency with a maximum at the lower end of the transect and a gradual decrease towards the upper limit; the distribution of *Hypodontolaimus zosterae* is similar but with much lower population densities.

On the upper transect the population densities of all species have been greatly reduced, but the intertidal distributions of *Viscosia viscosia*, *Anaplostoma viviparum*, *Theristus setosus* and *Sabateria* spp. are nevertheless quite interesting. *Anaplostoma viviparum* once again shows maximum population densities at a tidal level of about 10 ft above A C D, but *Sabateria* spp. here exhibits a distribution similar to this instead of the reverse type that it shows on the lower and middle transects. The intertidal distributions of *Viscosia viscosia* and *Theristus setosus* are peculiar in that both species have maximum densities at the ends of the transects, with low densities or complete absence in the middle.

In considering the distribution of species along the length of the estuary, it is not proposed to take the results for the middle reaches into account as only four quantitative samples were examined, and these were from widely different types of substratum. On the three transects, however, a total of thirty-two samples were examined quantitatively, and these yielded a total of thirty-seven species. The average population density of each species on each transect is given in Table 8, which shows that eleven species were common to all transects, seven were common to the middle and lower transects, two to the lower and upper transects and two to the middle and upper transects. Of the fourteen species restricted to one transect only, five were found on the lower, four on the middle, and five on the upper

transect. Three possible distributions in relation to distance from the sea are considered: population densities decreasing towards the head of the estuary; population densities increasing towards the head of the estuary; and a sporadic type of distribution, which is probably the combined result of insufficient sampling and the species concerned having low but fairly uniform population densities. Ten species, *Sphaerolaimus balticus*, *Paralinhomoeus lepturus*, *Oxystomatina elongata*, *Eutelolaimus elegans*, *Theristus* spp., *Leptolaimus setiger*(?), *Axonolaimus typicus*, *Paralinhomoeus elongatus*, *Chromadorina microlaima* and *Metalinhomoeus* spp. must be placed in this last group. There are seven species which are found on all three transects and which show a definite decrease in average population density towards the head of the estuary. The seven species found to be common to the lower and middle transects alone can be placed in this class with less certainty, while the inclusion of the five species found only on the lower transect must be tentative. On the other hand there are only two species common to all transects which show an increase in average population density towards the head of the

Table 7. *Nematode populations (per 100 cm²) on the middle and upper transects*

Each sample covered an area of 14·5 cm² and extended to a depth of 5 cm; in every case two subsamples were examined.

MIDDLE TRANSECT	Height of sample (ft) above Admiralty chart datum								
	11·2	9·95	8·7	7·3	5·8	4·7	4·15	3·4	2·95
Spirina parasitifera	1820	620	5960	5830	3800	1460	1560	410	–
Sabateria spp.	55	140	1110	1350	1650	3740	5500	4540	6440
Anaplostoma viviparum	5150	3720	5130	8000	3040	2150	3320	3220	6320
Hypodontolaimus zosterae(?)	165	–	380	725	755	1520	205	345	–
H. bütschlii	115	–	140	–	–	–	–	–	–
Theristus spp.	1280	350	275	725	415	340	620	690	230
Theristus setosus	270	620	275	–	–	70	–	70	–
Paralinhomoeus lepturus	445	–	1530	310	140	415	315	210	–
Enoplus brevis	390	1380	970	515	–	70	–	70	–
Odontophora armata	–	65	275	105	70	140	100	210	110
Sphaerolaimus balticus	–	65	–	105	70	70	100	70	350
S. hirsutis	–	–	–	–	–	–	–	70	–
Adoncholaimus fuscus	115	65	275	–	–	–	–	–	–
Thalassoalaimus tardus	115	–	–	–	70	140	205	70	–
Axonolaimus typicus	55	65	–	–	–	–	–	–	–
A. paraspinosus	–	–	–	–	–	–	–	70	–
Chromadorina microlaima	55	140	–	205	140	–	–	–	–
Monoposthia costata	–	65	–	–	–	70	–	–	–
Paracanthonchus caecus	–	65	–	–	–	–	–	–	–
P. elongatus	–	–	140	205	140	–	–	–	–
Halichoanolaimus robustus	–	–	140	–	–	–	–	70	–
Leptolaimus setiger(?)	–	–	–	–	70	205	830	960	230
Microlaimus tenuispiculum	–	–	–	–	70	340	100	–	–
Viscosia viscosia	–	–	–	–	–	70	415	275	350
Metalinhomoeus spp.	–	–	–	–	–	–	–	–	2350
Unidentified	270	140	1100	725	970	700	1030	550	1520
Totals	10 300	7500	17 700	18 800	11 400	11 500	14 300	11 900	17 900
Per cent of material examined	12·5	10·0	5·0	6·7	10·0	10·0	6·7	10·0	5·9
Number of nematodes examined	186	109	128	181	165	166	138	173	153
Estimated number of nematodes per sample	1490	1090	2560	2720	1650	1660	2070	1730	2600

UPPER TRANSECT	Height of sample (ft) above Admiralty chart datum								
	12·2	11·5	10·9	10·4	9·9	9·4	8·75	8·0	6·9
Spirina parasitifera	–	–	–	–	50	–	50	–	–
Sabateria spp.	50	145	2370	2980	2420	1680	590	960	95
Anaplostoma viviparum	50	50	185	480	2770	1970	1740	2880	240
Theristus spp.	95	95	245	290	305	145	–	95	–
Theristus setosus	480	–	290	95	50	–	50	95	1020
Thalassoalaimus tardus	385	50	530	335	240	290	480	50	–
Viscosia viscosia	1800	2270	2080	50	145	195	–	1100	435
Hypodontolaimus zosterae(?)	145	240	340	50	145	–	50	–	95
Oxystomatina elongata	145	485	485	50	100	240	1900	–	–
Tripyloides marinus	770	290	–	50	–	–	–	–	50
Enoplus brevis	–	–	45	145	240	145	190	–	–
Sphaerolaimus balticus	–	–	–	145	–	95	190	190	50
S. gracilis	–	–	–	–	–	–	–	50	–
Paralinhomoeus lepturus	–	–	–	50	240	145	95	50	–
Leptolaimus setiger(?)	–	–	–	50	–	–	95	–	–
Odontophora armata	–	–	–	–	100	–	–	–	–
Eutelolaimus elegans	–	–	–	–	50	–	190	–	–
Axonolaimus paraspinosus	–	–	–	–	–	–	50	–	–
Halalaimus gracilis	–	–	–	–	–	–	50	50	–
Spilophorella paradoxa	–	195	–	–	–	–	–	–	–
Adoncholaimus thalassophygas	–	–	–	–	–	–	–	–	95
Unidentified	680	430	580	380	145	195	190	480	200
Totals	4600	4250	7150	5150	7000	5100	4200	6000	2280
Per cent of material examined	14·3	14·3	14·3	14·3	14·3	14·3	14·3	14·3	14·3
Number of nematodes examined	95	88	148	107	145	106	87	125	47
Estimated number of nematodes per sample	665	615	1040	750	1020	740	610	875	330

estuary. Once again the three species common to the middle and upper transect can be included in this class only with less certainty than *Thalassoalaimus tardus* and *Theristus setosus* which were common to all three transects; the inclusion in this class of the five species found only on the upper transect must be tentative.

DISCUSSION

Free-living nematodes, being aquatic animals, live entirely surrounded by water, whether this be sea, river or estuarine. In an estuary the most variable factor in the habitat of the nematodes would be expected to be the salt concentration of the interstitial water of the mud in which they live. While other physical, chemical and biological factors in the interstitial water are possibly relevant, there is at present no evidence which shows the distribution of these factors in the estuary. It has been shown (Capstick 1957) that in the Blyth estuary the intertidal distribution of interstitial salinities at low spring tides is generally uniform with the exception of a small decrease at the upper and lower ends of the transects, and these deflections do not in themselves appear to be low enough to explain the intertidal distribution of the nematode population. However, these salinities were recorded after spring tides, and it is reasonable to assume that, as well-marked salinity stratification occurs in the estuary, salinities at both ends of the transects would be lower when the River Blyth is in spate during neap tides, when the

ratio of river to sea water is at a maximum. Perhaps under these conditions interstitial conditions at the upper and lower ends of the transects become limiting factors.

Table 8. *Average population densities (per 100 cm²) of thirty-seven species on the three transects*

	Transect			Notes
	Lower	Middle	Upper	
Spirina parasitifera	3700	2400	110	A
Sabateria spp.	6500	2700	1250	A
Anaplostoma viviparum	5100	4500	1150	A
Odontophora armata	340	120	10	A
Enoplus brevis	220	240	85	A
Hypodontolaimus zosterae(?)	1100	450	120	A
Axonolaimus paraspinosus	65	< 10	< 10	A
Thalassoalaimus tardus	85	65	260	B
Theristus setosus	20	145	230	B
Sphaerolaimus balticus	15	90	75	C
Paralinhomoeus lepturus	180	370	65	C
Hypodontolaimus bütschlii	350	280	–	A?
Adoncholaimus fuscus	35	50	–	A?
Sphaerolaimus hirsutus	< 10	< 10	–	A?
Monoposthia costata	25	15	–	A?
Halichoanolaimus robustus	< 10	20	–	A?
Microlaimus tenuispiculum	< 10	55	–	A?
Paracanthonchus caecus	< 10	< 10	–	A?
Metachromadora vivipara	50	–	–	A??
Theristus tenuispiculum	10	–	–	A??
T. acer	< 10	–	–	A??
Oxystomatina unguiculata	20	–	–	A??
Bathylaimus filicaudatus	< 10	–	–	A??
Oxystomatina elongata	65	–	380	C
Eutelolaimus elegans	< 10	–	25	C
Axonolaimus typicus	–	15	–	C
Paracanthonchus elongatus	–	55	–	C
Chromadorina microlaima	–	60	–	C
Metalinhomoeus spp.	–	260	–	C
Theristus spp.	–	550	140	C
Leptolaimus setiger(?)	–	250	160	C
Viscosia viscosia	–	120	900	B?
Adoncholaimus thalassophygas	–	–	10	B??
Sphaerolaimus gracilis	–	–	< 10	B??
Halalaimus gracilis	–	–	10	B??
Spilophorella paradoxa	–	–	20	B??
Tripyloides marinus	–	–	130	B??

–, not recorded at any of the points on the transect.
A, population densities decreasing towards head of the estuary.
B, population densities increasing towards head of the estuary.
C, sporadic distribution or not falling into A or B.
?, less certain inclusion in given class.
??, tentative inclusion in given class.

Conditions in other estuaries can be very different. Interstitial salinities of intertidal muds in the Tamar estuary were found by Smith (1956) to be uniformly distributed between high and low water marks at Salt Mill in June and October, but higher up the estuary the intertidal distribution was different and seasonal

variations were found. The general level of interstitial salinities was much lower in December than in June, and in the latter month salinities were highest at the top ends of the transects and lowest at the bottom ends, while in December this gradient was generally reversed. It is evident that the intertidal distribution of interstitial salinities in any given estuary will depend on its salinity characteristics, and these in turn will depend on such factors as volume and shape of the estuarine basin, relative volumes of salt and river water inflow as they change with time, and perhaps most important of all, whether salinity stratification occurs and when.

Schuurmans-Stekhoven (1935a) gives the distribution of *Enoplus brevis* as intertidal and sublittoral to a depth of 400 m, and Wieser (1952) gives the distribution of the closely related species *E. communis* as littoral and infralittoral to 3 m below A C D on seaweeds at Plymouth. On the evidence available for this and other countries members of this genus appear to be typically marine in character. The intertidal distribution of *E. brevis* on the three transects in the estuary is, however, unimodal (Fig. 3) with population densities falling at either end of the transects; the intertidal distribution of the remainder of the nematode population as a whole is similar, but not as distinct. As the members of this genus appear to be typically marine, it would be difficult to explain this distribution had it occurred on the sea shore rather than in an estuary. Under marine conditions one would expect populations to be similar in the littoral and infralittoral zone, and this is in fact what Wieser (1952) found to be the case for *E. communis* at Plymouth. It is therefore probable that some factor specifically connected with estuarine conditions is responsible for the intertidal distribution of *E. brevis* on the transects, and the most likely explanation is that the lower salinities in the tidal water at neap tides, particularly when the river is in flood, causes a greater decrease in the interstitial salinities at the lower ends of the transects than the recorded information, which was collected after spring tides, would suggest. The decrease in population densities at the upper ends of the transects could be caused by the low salinity of the surface layers at high tide affecting interstitial salinities, but the position is complicated still further by the gradual transition from a marine to a terrestrial habitat which occurs at this tidal level. Similar argument would explain the intertidal distribution of *Spirina parasitifera, Anaplostoma viviparum* and *Hypodontolaimus bütschlii* on the lower transect, of *Spirina parasitifera, Anaplostoma viviparum* and *Paralinhomoeus lepturus* on the middle transect, and *Anaplostoma viviparum* and *Sabateria* spp. on the upper transect. These can be considered as typically marine species, being influenced by the same factors that influence the intertidal distribution of *Enoplus brevis*. The intertidal distribution of *Sabateria* spp., *Hypodontolaimus zosterae*(?) and *Odontophora armata* on the lower transect, of *Sabateria* spp. and *Hypodontolaimus zosterae*(?) on the middle transect, and *Viscosia viscosia* and *Theristus setosus* on the upper transect would suggest that these species can tolerate, or actually prefer, habitats subject to variable salinity conditions, as they show maximum population densities at the lower ends of the transects, or in the case of *Viscosia viscosia* and *Theristus setosus* at both ends of the transects.

Schuurmans-Stekhoven (1935a) records these species (with the exception of *Hypodontolaimus zosterae*(?) which may be wrongly identified) as being found at various points on the North Sea coast and also in the Zuiderzee, where although salinities are fairly stable they are usually at a level below that of sea water. Of the species mentioned above, the one or more species included in the genus *Sabateria* have both types of distribution. On the lower and middle transects they have maximum population densities at the lowest intertidal levels, while on the upper transect they show a maximum in the middle of the transect. It is probable that this group of species can only tolerate a limited variation in interstitial salinity, and that conditions at the bottom end of the upper transect are outside the limits of their tolerance both with respect to variability and absolute level.

It has been shown that salinities of the tidal water at spring tides increase from

Table 9. *Mean interstitial salinities on the transects at different times of the year*

5% indicates that the 95% confidence limits do not overlap and the means are significantly different at this level.

	June	September	December	March
Lower transect	32·928 (33·877 – 31·979)	33·061 (33·269 – 32·852)	26·996 (27·808 – 26·184)	30·496 (31·434 – 29·558)
	– 5%	5%	5%	5%
Middle transect	31·872 (32·644 – 31·100)	31·583 (31·823 – 31·343)	24·144 (25·368 – 22·920)	24·505 (26·391 – 22·619)
Lower transect	32·928 (33·877 – 31·979)	33·061 (33·269 – 32·852)	26·996 (27·808 – 26·184)	30·496 (31·434 – 29·588)
	5%	5%	5%	5%
Upper transect	30·161 (30·923 – 29·399)	32·161 (32·481 – 31·841)	24·344 (25·174 – 23·514)	22·044 (23·866 – 21·222)
Middle transect	31·872 (32·644 – 31·100)	31·583* (31·823 – 31·343)	24·144 (25·368 – 22·920)	24·505 (26·391 – 22·619)
	5%	5%	–	–
Upper transect	30·161 (30·923 – 29·399)	32·161* (32·481 – 31·841)	24·344 (25·174 – 23·514)	22·044 (23·866 – 21·222)

* Mean salinity higher on the upper transect.

the surface to the bottom and from the head of the estuary to the sea (Capstick 1957). Although the salinity of the tidal water decreases towards the head of the estuary at high tide, it does not follow automatically that a corresponding decrease occurs in the salinity of the interstitial water of muds along the length of the estuary. Furthermore, until it is possible to follow the variations in interstitial salinities throughout many complete tidal cycles, the effect of variations in the salinity of the tidal water can only be deduced from interstitial salinities taken when the mud is exposed, and naturally this method can only give part of what is obviously quite a complicated story. Information about interstitial salinities in the estuary is available for the three transects, and these results were taken at or near low water of spring tides. It has already been stated that there was little variation in the intertidal distribution of these salinities under this set of conditions, so it is reasonable to average the results for each transect and to compare the means. This procedure has two disadvantages: results for each transect were

not collected on the same day but all were collected within 3 or 4 days; secondly, as the results were collected at low tide, each sampling point had been exposed for a different time before sampling (this interval being largest at the upper ends of the transects and smallest at the lower ends), and during summer and autumn exposure has been shown to produce increases in the salinity of interstitial water. However, bearing these points in mind it will be seen from Table 9 that in general interstitial salinities decrease towards the head of the estuary, although the

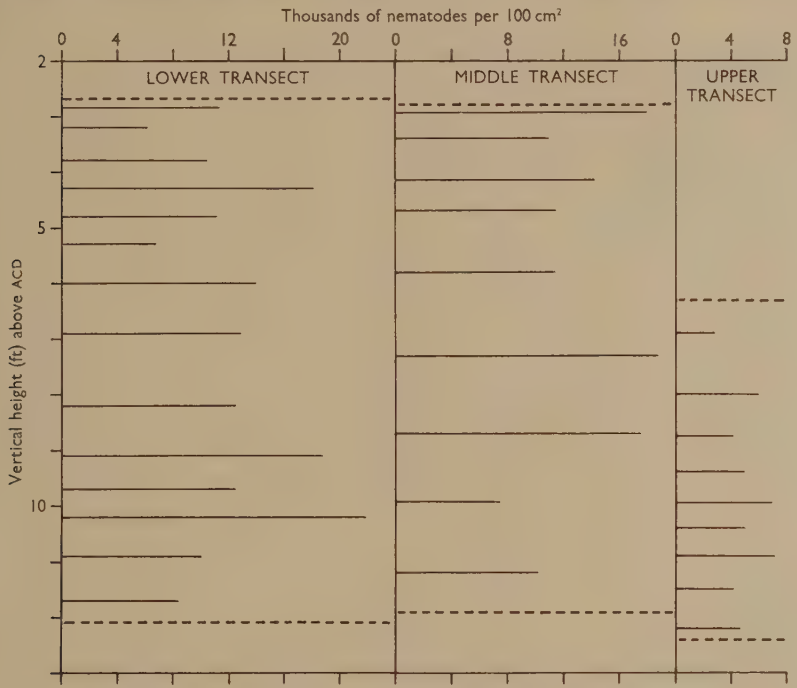

Fig. 4. The intertidal distribution of the total nematode populations on the transects. Horizontal broken lines show the upper and lower limits of the transects.

differences are smaller than would be expected from a consideration of salinities of the tidal water at high tide. The mean interstitial salinities on the lower transect were significantly greater than those on the upper transect at the 5% level of probability for all months quoted. The differences between the means for the middle and upper transects were not so consistent. In June the mean for the middle transect was significantly greater than that of the upper transect, while in September it was significantly lower, and there was no difference in December and March. The means from the lower transect were significantly greater than those from the middle transect in September, December and March but not in June. Interstitial salinities collected after neap tides would be expected to give similar differences, but mean salinities would be at a lower absolute level.

Table 10. *The geographical distribution of the species found in the estuary*

(M.R.) = Middle reaches. L. = Lower transect. M. = Middle transect. U. = Upper transect.

	Blyth estuary	Dutch coast	Zuiderzee	Coast of Belgium	German N.S. coast Heligoland, Jutland	Channel coast of England	On algae, rocky coast, Plymouth	Channel coast of France	Northumberland and Durham coast	Atlantic coast of Ireland
Thalassoalaimus tardus de Man	M.R. L.M.U.	–	–	–	+	+	+	–	–	–
Oxystomatina elongata (Bütschli)	M.R. L.U.	–	–	–	+	+	–	–	+	–
O. unguiculata Schuurmans-Stekhoven	L.	–	–	–	–	–	–	–	–	–
Trefusia longicauda de Man	(M.R.)	–	–	–	–	–	–	–	–	–
Halalaimus gracilis de Man	U.	–	–	–	–	–	–	–	–	–
Enoplus brevis Bastian	(M.R.) L.M.U.	–	–	–	–	–	–	–	–	–
Anaplostoma viviparum Bastian	(M.R.) L.M.U.	–	–	–	–	+	–	+	–	–
Viscosia viscosia (Bastian)	(M.R.) M.U.	–	–	–	–	+	–	+	–	–
Adoncholaimus thalassophygas (de Man)	U.	–	–	–	+	–	–	–	–	–
A. fuscus (Bastian)	(M.R.) L.M.	–	–	–	+	+	–	+	–	–
Paracanthonchus elongatus (de Man)	M.	–	–	–	–	–	–	–	–	–
P. caecus (Bastian)	L.M.	–	–	–	–	+	+	–	–	–
Halichoanolaimus robustus (Bastian)	(M.R.) L.M.	–	–	+	–	+	+	–	–	+
Monoposthia costata (Bastian)	(M.R.) L.M.	–	–	+	–	+	+	–	–	–
Metachromadora vivipara (de Man)	L.	–	–	–	–	–	–	–	–	–
Spirina parasitifera (Bastian)	(M.R.) L.M.U.	–	–	–	–	–	–	–	–	+
Microlaimus tenuispiculum de Man	L.M.	–	–	–	–	–	–	–	–	–
Spilophorella paradoxa (de Man)	U.	–	–	–	–	–	+	–	–	–
Chromadorina microlaima (de Man)	M.	+	–	–	–	+	–	–	–	–
Hypodontolaimus inaequalis (Bastian)	(M.R.)	–	–	–	–	+	+	–	–	–
H. bütschlii Filipjer	(M.R.) L.M.	–	+	–	–	–	–	–	–	–
H. zosterae Allgen(?)	L.M.U.	–	–	–	–	–	–	–	–	–
Ascolaimus elongatus (Bütschli)	(M.R.)	–	+	–	–	–	–	–	+	–
Odontophora armata (Ditlevsen)	(M.R.) L.M.U.	–	–	–	–	–	–	–	–	
Axonolaimus typicus de Man	M.	–	–	–	–	–	–	–	–	–
A. paraspinosus Schuurmans-Stekhoven & Adam	L.M.U.	–	–	–	–	–	–	–	–	–
Leptolaimus setiger Schuurmans-Stekhoven & De Coninck(?)	M.U.	–	–	–	–	–	–	–	–	–
Eutelolaimus elegans de Man	L.U.	–	–	–	–	–	–	–	–	–
Bathylaimus filicaudatus Schuurmans-Stekhoven & Adam	L.	–	–	–	–	–	–	–	–	–
Tripyloides marinus (Bütschli)	(M.R.) U.	–	–	–	–	–	–	–	–	–
Paralinhomoeus lepturus de Man	L.M.U.	–	–	–	–	–	+	–	–	–
Theristus setosus (Bütschli)	L.M.U.	–	–	–	–	–	+	–	+	–
T. tenuispiculum Ditlevsen	L.	–	–	–	–	–	–	–	–	–
T. acer Bastian	(M.R.) L.	–	–	–	–	+	+	–	+	+
Sphaerolaimus gracilis de Man	U.	–	–	–	–	–	–	–	–	–
S. hirsutis Bastian	(M.R.) L.M.	–	–	–	–	–	–	–	–	–
S. balticus G. Schneider	L.M.U.	–	–	–	–	–	–	–	–	–
Total number of records	37	28	27	23	17	15	11	10	6	4

There is, therefore, evidence that in the middle and upper reaches of the estuary, interstitial salinities decrease towards the head of the estuary. As a corresponding decrease has been shown to occur in the numbers of adult *Enoplus brevis* (Fig. 3) and also in the nematode population as a whole (Fig. 4) it is likely that the decrease in population densities and interstitial salinities is interrelated and that somewhere in the estuary, near the level of the upper transect, interstitial salinities are a significant (if not a limiting) factor in the distribution of the estuarine free-living nematode population. This, of course, implies that the nematodes considered are primarily marine species, and there is some evidence to support this hypothesis. Table 10 presents a complete list of all positive identifications made, and brings up to date the information on distribution given in Schuurmans-Stekhoven (1935a) for these species. Out of the thirty-seven species recorded in the Blyth estuary twenty-eight have been previously recorded from the Dutch coast, twenty-three from the Belgian coast and twenty-seven from the Zuiderzee. Apart from the other records from the marine habitats given in this table, sufficient others are given by Schuurmans-Stekhoven (1935a) to indicate that most of the thirty-seven species found have the cosmopolitan, marine type of distribution, but that they are also to be found in such areas as the mouth of the Baltic and the northern part of the Zuiderzee where reduced salinities are encountered. There is an insufficient number of records to show whether or not a definite brackish water fauna exists, but in my opinion this is unlikely. The nematode fauna dealt with in this paper is probably marine in its origins and the fact that members of a marine fauna have been shown to exist in large numbers at the head of the Blyth estuary is due partly to the salinity characteristics of the interstitial water and partly to the well-known ability of nematodes to colonize almost every available habitat.

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SUMMARY

1. Two extraction techniques are described, one used for the large *Enoplus brevis* and the other for the total nematode population. The results are tested for consistency and significance.

2. The nematode populations at six stations in the middle reaches increase with the amount of mud in the substratum.

3. The intertidal population densities of *E. brevis* on three transects in the upper reaches decrease at the upper and lower ends of the transects, and as the head of the estuary is approached; it is suggested that this is due to the limiting effect of interstitial salinities.

4. The intertidal distributions of the individual species forming the population are recorded for each transect and, collectively, show similar reductions at the upper and lower ends of the transects and towards the head of the estuary.

5. Average population densities of most species fall towards the head of the estuary, but a few show the reverse type of distribution. This evidence, and the recorded geographical distribution of the species concerned, suggests that the nematode population of the estuary is primarily marine in origin.

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ALARY POLYMORPHISM IN THE GERROIDEA (HEMIPTERA-HETEROPTERA)

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(With 1 Figure in the Text)

Very little attention has been paid to the biology of the British water-bugs other than the Corixidae, although there are a few, easily identifiable, species. Alary polymorphism in the group has been studied widely on the Continent, principally in its genetical aspects. Mitis (1937) suggested that a study of polymorphism in relation to life-cycles, habitat and distribution would be profitable. The following observations were made in the course of a two-year study of these insects in 1956-8. Details of habitat and distribution will be presented elsewhere (Brinkhurst 1959). Species having similar patterns of life-cycle and polymorphism are considered together under the headings: univoltine species, which may be apterous or macropterous, and bivoltine species, which may be dimorphic or polymorphic.

METHODS

All records of adults and nymphs are based on collections made with a D-ended pond-net (as supplied by the Freshwater Biological Association) in a standard period of 15 min. Although this method is open to criticism, no better way could be devised of obtaining comparable samples of these active insects from the wide variety of habitats involved. It is possible to obtain random samples of the various polymorphic forms of adults, but there is a bias towards the capture of adults and older instars, as younger nymphs occur nearer to the shore than most of the population.

The determination of nymphal instars, and the sex and polymorphic forms of the adults, was carried out in the field so that it was possible to return a high proportion of the catch to the water. It was of course necessary to determine the identity of the nymphs in populations of more than one species (Brinkhurst, in press, b). Samples of the populations were retained for laboratory examination, estimates of the maturity of these samples being obtained by dissection. When eggs were present but not fully developed, the females were termed semi-mature, and mature and immature specimens are self-explanatory. The presence or absence of wing muscles in macropters throughout the year was recorded. A record was kept of the development of the wings in short-winged forms. The following scheme was adopted, after Poisson (1924):

Apter where the wings reached the posterior end of the tergum 2
Micropter where the wings reached the posterior end of the tergum 3
Sub-brachypter where the wings reached the posterior end of the tergum 4

Brachypter where the wings reached the posterior end of the tergum 5
Sub-macropter where the wings reached the anterior end of the tergum 7
Macropter where the wings reached beyond the anterior end of the tergum 7

In the following account the 1957 data is usually quoted, as in all species the second year's data expanded the 1956 observations. Full details of these earlier collections appear elsewhere (Brinkhurst 1958).

LIFE-CYCLES AND THE OCCURRENCE OF ALARY POLYMORPHISM

(*a*) *Apterous univoltine species*

Velia caprai Tam. Only adults are obtainable in early spring, the first nymphs being captured in May. Copulation was observed in April and May when

Table 1. *Captures of* Velia caprai *on Claife Heights during 1957*

	Males	Females	Maturity*	Nymphs			
				5	4	3	1+2
22 Apr.	7	10	M	–	–	–	–
7 May	5	17	M	–	–	–	15
21 May	4	8	M	–	–	–	35
11 June	–	2	M	2	20	21	6
24 June	2	1	I	57	58	30	10
8 July	17	17	I	81	38	7	5
23 July	8	14	I	25	10	4	–
3 Aug.	14	11	I	67	9	5	–
17 Aug.	12	18	I	5	–	–	

* M, mature; I, immature.

mature females contained up to sixteen eggs. The site of oviposition was not observed although both moss and stones were searched. Mature females lived longer than males, as shown in Table 1 and also by collections made in 1956, when in May 41 males and 187 females were captured as compared with the 1 : 1 ratio of the sexes in all other months. First instar nymphs were observed in May and occurred commonly in June, and the data in Table 1 indicate that these formed the single annual generation. Immature adults were obtained as early as 8 July.

Only three macropterous specimens were observed in the course of 2 years' collecting, although a total of 731 insects were examined. Apterous males were seen in copulation with these macropters which were all females. They were collected on a mountain stream at Abergwesyn, Brecknock, on 11 April 1957. Walton (1943) also recorded copulations between apters and macropters. Two further macropterous females were observed in April 1958 on the Silverburn, Ballasalla, Isle of Man. Dr H. B. N. Hynes (personal communication) tells me that macropters are relatively common on the island. The rare macropterous individuals of this predominantly apterous species assist in furthering its distribution, and this may account for the increase in macroptery on the Isle of Man.

Velia saulii Tam. The evidence in the literature and a few personal observations suggest that both *Velia* species have similar life-cycles. The only records of polymorphism are those given by Brown (1954) who cites nine macropters and thirty apters. I have only found apterous specimens.*

Gerris najas Deg. Mitis (1937) described this species as univoltine, nymphs being present from June onwards, the new generation of adults appearing in August-September. Observations recorded in Table 2 confirm that the species is univoltine and that, as in all other species considered here, the adults overwinter. They may reappear on the water as early as February (Scudder 1956) but are not common until March. They pair in April, remaining paired right through the day but separating in the dark. The eggs are laid on stones beneath the water as described elsewhere (Brinkhurst, in press, a).

Table 2. *Total numbers of* Gerris najas *in Boathouse 1 (High Wray) during 1957*

	Males	Females	Maturity*	Nymphs			
				5	4	3	1+2
1 Apr.	2	6	S	–	–	–	–
25 Apr.	3	9	S	–	–	–	–
6 May	4	8	S	–	–	–	–
22 May	1	3	S	–	–	–	–
8 June	2	4	M	–	–	–	–
16 June	2	4	M	–	–	–	30
21 June	2	4	M	–	–	17	18
30 June	2	4	M	–	3	44	14
12 July	2	2	M	25	33	49	21
19 July	–	1	M	28	35	17	12
2 Aug.	23	10	I	16	18	38	61
17 Aug.	32	26	I	23	33	13	2
6 Oct.	78	55	I	2	–	–	–

* Based on collections from other boathouses.
S, semi-mature; M, mature; I, immature.

Immature adults of the new generation were obtained on 2 August 1957 in a boathouse on Windermere. These were marked with spots of nail-varnish, released, and subsequently recaptured in the same boathouse in the following spring. This observation, coupled with the fact that these insects inhabit only those boathouses constructed of local stone by the dry-stone technique, and not those made of smooth stones or concrete, leads me to suppose that they overwinter in the numerous crevices in the walls of the local stone boathouses. They have also been observed to retreat deep into the boathouse when disturbed or at the onset of cold, wet, or windy weather.

Macropters have been recorded by Butler (1923), Poisson (1924, 1951), and Massee (1954). Poisson (1951) stated that macropters were common in the Pyrenees, forming separate colonies from the apters. Most accounts of the species list only apterous captures (Jaczewski 1934) and although I have collected more than 2000 individuals I have not obtained one macropter.* It is clear that, as in *Velia*, macroptery plays no regular part in the biology of this species.

* Recent collections included normal macropters (Brinkhurst, in press).

(*b*) *Macropterous univoltine species*

Gerris costai (H.-S.). Mitis (1937) stated that this species was univoltine and my own scanty records support this view. The species occurs commonly at high altitudes in northern Britain and so was not available for regular sampling. Mature adults were collected in May along with nymphs, and the latter occurred alone in early July. By late July and August all adults were immature, and as overwintering begins in September (Butler 1923) there is no second generation.

Jordan (1947) recorded micropters and apters but described these as rare, and only macropters have been recorded in Britain so far. I obtained two sub-macropters in Glen Tromie, Easterness, in August 1958, but in general this species is monomorphic with no regularly occurring alternative forms.

Gerris gibbifer Schum. Semi-mature specimens of this species were observed in copula in late April 1957 (Table 3). Mature specimens were observed from May until 12 June in decreasing numbers, most females containing twenty-four eggs.

Table 3. *Captures of* Gerris gibbifer *at Haverthwaite in 1957*

	Macropters		Sub-macropters		Wing muscles of Macropters		Maturity	Nymphs			
	Males	Females	Males	Females	–	—		5	4	3	2+1
26 Apr.	24	24	1	2	8	1	S	–	–	–	–
9 May	15	21	2	3	12	1	M	–	–	–	1
24 May	22	24	–	4	9	3	M	–	–	–	–
12 June	12	7	–	3	8	0	M	–	2	2	40
24 June	–	–	–	–	–	–	–	4	10	–	12
8 July	2	5	–	–	2	0	I	19	15	16	7
21 July	3	6	–	–	6	0	I	40	19	3	–
3 Aug.	27	16	–	1	16	0	I	7	1	–	–

First instar nymphs were present from 12 June and later instars became commoner during August, after which all adults were immature. The data clearly show that this species is univoltine, contrary to the views of Mitis (1937), who correlated the occurrence of light-coloured individuals in the summer with a second generation but cited no other evidence. Whilst it is true to say that, in the summer generation of bivoltine species the individuals are lighter than those of the winter generation, all such specimens of this species proved to be teneral as they darkened in the laboratory. Gulde (1921) described a 'var. *flaviventris*' which may also be a developmental stage, the teneral condition being more obvious and of a longer duration than in other species.

Jordan (1947) was the first to record the short-winged submacropterous form of this species and Forster (1954) studied a population containing 38% submacropters during the period March-May 1954. He found a closely similar percentage in the following generation in the autumn, showing that Ekblom (1941) was wrong in assuming that his laboratory experiments proved that short-winged forms survived the winter better than the macropters (see p. 223). The apparent increase in the percentage of short-winged forms in the spring and autumn

(illustrated in *G. lacustris*—Fig. 1) Forster explained as the landward migration of macropters to terrestrial overwintering sites and their later arrival on the water in the following spring (see *G. lateralis*, *G. lacustris*). My records of *G. gibbifer* in 1956-7 reveal a much smaller percentage of short-winged forms than recorded by Forster (1954), as 21 sub-macropters and 367 macropters were seen, although many individuals were recorded more than once owing to the technique of replacing individuals after examination. Seven of the sub-macropters had no wing muscles at a time when all the macropters possessed them. Although this species is regarded as macropterous in this work, it should be noted that short-wingedness is commoner than in other monomorphic species. The significance of the short-winged form in a univoltine species is not clear unless it serves to maintain that species on a suitable habitat from one season to the next, the long-winged form overwintering far from the summer habitat.

(*c*) *Dimorphic bivoltine species*

Gerris odontogaster (Zett.). This species has been described as bivoltine by Jordan (1929) and later authors, and the data obtained during the present survey support this view (Table 4). The overwintering generation produced nymphs in

Table 4. *Captures of* Gerris odontogaster *on Claife Heights during 1957*

	Macropters		Micropters		No. of Macropters examined	No. of Macropters without wing muscles	Maturity	Nymphs			
	Males	Females	Males	Females				5	4	3	2+1
2 Apr.	39	29	–	–	15	2	S	–	–	–	–
22 Apr.	25	20	–	–	10	3	S	–	–	–	–
6 May	8	9	–	–	11	5	S	–	–	–	–
20 May	4	14	–	–	11	10	M	–	–	–	–
11 June	–	4	–	–	4	4	M	–	8	8	16
25 June	–	2	8	9	2	0	M	32	38	6	–
8 July	4	–	–	3	1	1	M	9	6	29	37
21 July	11	7	2*	1	15	6	I	8	38	16	7
3 Aug.	7	6	–	–	4	0	I	6	–	–	–
17 Aug.	19	19	–	1	30	14	I	46	33	11	6
26 Sept.	24	32	–	–	15	1	I	20	3	2	–

* Includes one brachypter.

early June, and these developed into the summer generation at the end of that month. The micropters of this generation matured, and therefore probably developed, earlier than the macropters. Early instar nymphs found from July onwards produced the second, overwintering, generation in August and September. Flight was observed in April (Dr C. H. Fernando, personal communication) but was rare in other months. The method of trapping used attracted water-seeking insects and so missed the landward autumn flight. All macropters possess wing muscles in the autumn and early spring when they are immature, but after the

post-overwintering flight in April the insects resorb the wing muscles while they are maturing the gonads. Table 4 records the presence and absence of wing muscles in macropters and clearly illustrates this correlation with maturity.

Ekblom (1928) described two forms of *G. odontogaster*, the macropter and the micropter. Brachypterous forms have been recorded but are rare; only one was collected in the present study. Jordan (1943) recorded a range of forms including apters, and claimed that micropters were commoner in the north and in cold situations. Ekblom (1950) did not accept this, claiming that there was a possibility of a single generation under such circumstances. Leth (1943) recorded 'brachypters' in July and August and confirmed that these were absent in the overwintering generation. I found that micropters formed half of the rather small populations from which samples were collected in 1956, becoming scarce in August and September (Brinkhurst 1958). Similar results were obtained in 1957, with the June and July figures again rather low but containing all but one of the records of micropters, and one brachypter (Table 4).

Although the life-cycle has been described before it has not been clearly stated that all short-winged forms appear in the summer generation and are therefore produced by the overwintering macropters. My own records indicate that the

Table 5. *Records of* Gerris argentatus *from Pull Wyke, Windermere, in 1957*

	Macropters		Micropters		No. of Macropters without wing muscles	Maturity	Nymphs			
	Males	Females	Males	Females			5	4	3	2+1
23 Apr.	9	16	–	–	0	I	–	–	–	–
10 May	12	5	–	–	0	S	–	–	–	–
22 May	9	10	–	–	19	S	–	–	–	–
8 June	7	9	–	–	15	M	–	–	–	–
24 June	8	12	–	–	20	M	–	–	28	35
6 July	7	8	–	–	15	M	10	5	3	7
19 July	5	1	9	10	2	M	14	3	27	14
2 Aug.	7	14	–	2	0	I	24	–	–	–
17 Aug.	23	11	–	1	0	I	6	1	3	1
26 Sept.	24	32	–	–	0	I	20	2	1	–

micropters emerge earlier in the year than the macropters of the same generation, and this, together with the suggestion that short-winged forms are commoner in cold situations, has considerable significance in the study of alary polymorphism.

Gerris argentatus Schum. Butler (1923) described this species as univoltine as there were no records of mature adults in July, but Mitis (1937) described two distinct generations in Germany. My own records indicate that there is a summer generation which becomes adult in July and early August, and a second generation, developing in September, which overwinters and breeds in the following spring (Table 5). The maximum number of eggs recorded in a female was twenty-seven, most mature individuals containing twenty-four. Nymphs were seen for the first time on 24 June, a fortnight after fully mature forms were common in the population. Early instar nymphs were absent on 2 August but were seen again in

subsequent collections. The wing muscles of the macropters were resorbed by late May, those of the summer generation generally had wing muscles present. Flight was observed in the laboratory on 10 May 1957.

Mitis (1937) related the life-cycle to polymorphism in this species by stating that the first generation was entirely apterous, the second macropterous. Leth (1943) records a much smaller percentage of brachypters and micropters (as opposed to macropters) during July and August. Jordan (1947) described micropters

Table 6. *Captures of* Gerris paludum *at Fourwents Pond, Surrey, in 1956*

	Macropters		Brachypters		Nymphs			
	Males	Females	Males	Females	5	4	3	2+1
28 Apr.	–	–	–	–	–	–	–	–
22 May	4	4	–	–	–	–	–	–
22 July	–	–	12	12	17	21	13	8
24 Aug.	1	4	–	–	3	7	–	–
29 Sept.	7	9	–	–	10	5	5	6
23 Oct.	1	1	–	–	–	–	–	–

and brachypters as rare, the predominant form being the macropter. Unfortunately, only small numbers of adults were captured in the significant months of July and August, owing in part to a low rainfall in the early summer which adversely affected most gerrid populations in 1957. The figures do indicate (Table 5) that micropters occurred only in the summer generation, and that macropters overwintered alone. The large number of micropters taken on 19 July is indicative of the fact that the short-winged forms are the first to develop in the summer generation, as in *G. odontogaster*. The second generation was seen to be entirely macropterous in contrast to this mixed first generation.

Table 7. *Captures of* Gerris thoracicus *at Moreton, Cheshire, 1957-8*

	Macropters		Sub-macropters		Macropters without wing muscles	Maturity	Nymphs			
	Males	Females	Males	Females			5	4	3	2–1
4 Oct. 57	24	52	0	0	0	I	0	0	0	0
7 May 58	5	6	0	0	0	I	0	0	0	0
10 June 58	2	2	0	0	4	M	0	2	0	1
14 July 58	3	4	1	4	0	S	24	5	0	0
21 Aug. 58	16	16	2	7	1	Mac: I (one M) Sub-mac: M	24	53	42	40
2 Oct. 58	18	34	0	0	0	I	9	0	0	0

Gerris paludum (Fab.). Mitis (1937) described two generations, very distinct in their polymorphic form. My own observations indicate that Mitis was correct as, although the numbers recorded are small, they represent almost the entire population of Fourwents Pond, Dorking (Table 6). Short-winged adults collected with nymphs in July did not form part of the autumn population observed in September, which contained a second set of nymphs. Adults appeared later in the year than in other species, and the summer generation seems to live only 2-3 weeks.

There have been no British records of the brachypterous form of *G. paludum* although they have been recorded on the Continent by many authors. Mitis (1937) claimed that the first generation was entirely brachypterous, the second entirely macropterous, and the present data support this view, as all twelve adults taken on 22 July were brachypters. These individuals were replaced on the pond but did not form part of later populations. This was also true of the five macropters seen on 24 August and it is possible that these formed the macropterous part of the summer generation, in which case they developed much later than the brachypters.

Gerris thoracicus Schum. In a previous account this species was thought to be univoltine, but more detailed observations made during 1957-8 at Moreton, Cheshire (Table 7), have indicated that Mitis (1937) was correct in assuming that this species was bivoltine. Adults developing in July breed to produce an immature macropterous generation in August-September, all sub-macropters collected on 21 August being mature, first-generation adults.

Walton (1943) and Jordan (1947) regarded this species as macropterous, but my own studies indicate that a sub-macropterous form occurs in the summer generation in this bivoltine species, as in the previous two instances.

(*d*) *Polymorphic bivoltine species*

Gerris lacustris L. Mitis (1937) and Larsen (1950) observed that *G. lacustris* was bivoltine, and the present observations (Table 8) support that view. Overwintered adults appeared during April, often with quantities of dust and soil on them. This was observed in both 1956 and 1957, and it is considered that these

Table 8. *Captures of* Gerris lacustris *on Claife Heights, N. Lancs., in 1957*

	Macropters		Brachypters		No. of macropters	No. of macropters without wing muscles	Maturity	Nymphs			
	Males	Females	Males	Females				5	4	3	2+1
2 Apr.	–	4	3	13	4	–	S	–	–	–	–
22 Apr.	39	65	42	40	10	–	S	–	–	–	–
7 May	93	117	49	51	14	2	M	–	–	–	–
21 May	69	86	44	30	22	21	M	–	–	–	–
11 June	11	14	6	3	19	18	M	–	–	2	28
25 June	9	14	5	6	15	15	M	35	42	14	19
8 July	24	12	36	56	10	7	I+M	160	151	68	32
23 July	41	31	9	13	20	11	I	43	11	64	38
3 Aug.	21	29	10	9	25	1	I	15	4	2	17
17 Aug.	42	29	13	10	20	–	I	130	78	11	6

insects had overwintered on land. Douglas (1882) recorded hibernating macropters a long distance from water and two macropterous adults were captured near Box Hill by Mr J. H. P. Sankey (Brinkhurst 1956) far from the nearest population of this species on the River Mole. One female macropter was beaten out of an oak tree at Wytham, Oxford, in September by Dr A. F. G. Dixon (personal communication). Copulation was observed in April and May. The males matured before the females (indicated as semi-mature in April, Table 8), but the females lived longer.

Thus, in May 1956, 227 males were taken compared with 357 females, in contrast to the normal 1 : 1 ratio in all other months. Eggs were laid in the laboratory on 21 May, and took from 10 to 20 days to hatch. Details of the egg numbers in mature macropterous and brachypterous females are shown in Table 9. This

Table 9. *Eggs contained by mature females of* Gerris lacustris

Number	Macropters	Brachypters	Number	Macropters	Brachypters
10	1	–	23	7	2
11	–	1	24	10	5
12	–	2	25	1	1
13	–	1	26	1	–
14	3	5	27	2	1
15	2	–	28	–	1
16	1	1	29	–	1
17	2	2	30	–	1
18	2	1	Others	37–1	–
19	4	2	Mean	21·3	20·2
20	6	3			
21	2	3			
22	3	3			

shows that twenty-four is approximately the mode in both cases, though the means are a little lower. This is probably due to the inclusion of some semi-mature individuals in the samples as well as a few which had already laid some eggs. Applying a t test to these figures with the hypothesis that there was no difference between long- and short-winged females, gave t as 1·16 with 82 degrees of freedom, and as this is well within the 5% value, the hypothesis is accepted.

Table 10. *Wing-length frequency in short-winged* Gerris lacustris

	Abdominal tergite	Females	Males	Total	Group total
Apters	P2	2	–	2	2
Micropters	A3	–	–	–	5
	M3	–	3	3	
	P3	–	2	2	
Sub-brachypters	A4	–	7	7	30
	M4	2	6	8	
	P4	3	12	15	
Brachypters	A5	2	11	13	117
	M5	16	37	53	
	P5	31	20	51	
Sub-macropters	A6	15	7	22	47
	M6	10	4	14	
	P6	6	1	7	
	A7	3	1	4	
Total		90	111	201	

Eggs laid in May give rise to nymphs in June, the adults from which formed the first generation. Nymphs were present in the collections up to the end of the year, large numbers of fifth-instar nymphs being seen from August onwards. These gave rise to the second-generation adults in August and September.

G. lacustris was shown to be a truly polymorphic species by Poisson (1924, 1951),

all forms from apters to macropters being observed, and this was confirmed by Jordan (1947). The frequency of the various wing lengths in the two sexes in 1956-7 is recorded in Table 10. Statistical tests were carried out to ascertain the difference in wing length in short-winged males and females. These gave a χ^2 of 25·168 with 3 degrees of freedom. The tabulated value of χ^2 with 3 d.f. is 7·81, and so there is a significant difference in the wing lengths of males and females. Poisson (1924) and Mitis (1937) described the increase in short-winged forms in the summer, the latter associating it with the appearance of the first generation. *G. lacustris* and the following *G. lateralis* are distinct in that as well as having a wide range of polymorphic forms they have a small percentage of short-winged forms in the winter generation. The significance of this will be discussed in the second section of this paper.

The results of fortnightly samples appear confusing at first sight as the percentage of short-winged forms rises and falls throughout the year (Fig. 1) in an apparently irregular manner. If we first consider the percentages from May to

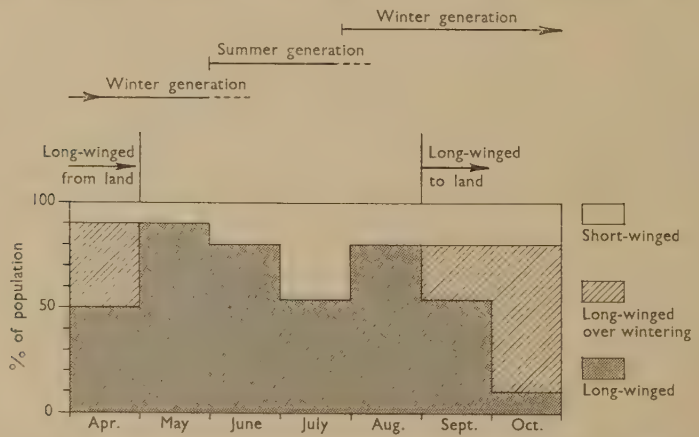


Fig. 1. The life-cycle and polymorphism in *Gerris lacustris*, the latter expressed as percentage composition of the population.

August inclusive, the pattern is that of the dimorphic species other than *G. paludum* with a large percentage of short-winged forms in the summer generation, but a small percentage in the overwintering generation in addition. The apparent fall in the percentage of long-winged forms in earlier and later months is due to the fact that these insects overwinter on land, the macropters often going far from water and flying from the pond earlier and returning later in the spring than the brachypters. Similar observations were made by Forster (1954) in *G. gibbifer* (see above) and it is clear that in both these species the percentage of short-winged forms is unchanged during overwintering, and therefore the significance of the short-winged form cannot be its powers of survival through the winter (Ekblom 1941).

Gerris lateralis Schum. No account of the life-cycle is available except that of Ekblom (1941) whose collections did not extend into the summer. There is the usual increase in short-winged forms in the summer, associated with a small percentage of these in the winter. The results of Ekblom's collections (Table 11) show the same pattern of increase of long-winged forms from April to June as discussed above (see *G. lacustris*) and so one can safely assume that this species has a closely similar cycle to that of *G. lacustris*.

Jordan (1947) stated that macropters were rare, apters and micropters common, and Leth (1943) collected 339 short-winged forms and only 36 long-winged. Ekblom (1941, 1949) carried out a detailed investigation of polymorphism in this species. He claimed that short-winged forms were commoner in the spring, his figures (which I summarize) being shown in Table 11. Ekblom interpreted these results as illustrating a selective advantage to the short-winged form during overwintering. A similar increase in the proportion of short-winged forms of *G. lacustris* was observed here in April, but was ascribed to the fact that the macropters fly to land in the autumn, returning to the water in the spring. The short-winged

Table 11. *The occurrence of polymorphic forms of* Gerris lateralis

	Macropters	Micropters	Apters
April	16	0	30
May	98	2	35
June	19	0	9

forms stay on the water later in the year and emerge earlier, as they can probably withstand temperatures lower than that at which flight becomes impossible. Similar observations were made on *G. gibbifer* by Forster (1954). Ekblom carried out an experiment in which macropters and apters were confined in tanks at a low temperature, and the apters survived far better than did the macropters. He claimed that this showed that the short-winged forms overwintered more easily in the field, and that in this lay the significance of polymorphism in the biology of the species. In fact this ignores the conditions applying in the field where the macropters can fly to find suitable overwintering sites, the flightless forms having to make use of whatever shelter there is around the habitat. That cold-hardiness has a survival and therefore a selective value for short-winged forms in these circumstances is hardly surprising, as this is considered to be the correct interpretation of Ekblom's results.

(*e*) *Summary*

All *Gerris* and *Velia* species overwinter in the adult phase, maturing and breeding in the following spring. They are either univoltine or bivoltine, but only the bivoltine species are truly polymorphic. Univoltine species living on rivers and streams are apterous whilst those inhabiting ponds or lake margins are macropterous. In most bivoltine species, polymorphic forms occur only in the summer generation and are therefore produced by the overwintered adults. In two species

(*Gerris lacustris*, *G. lateralis*) there is an increase in polymorphism in the summer generation but a small percentage of short-winged forms in the winter generation. It will be shown below that there are two distinct mechanisms of determination of alary polymorphism, one of which applies to the winter-generation short-winged forms in these two species alone. These findings are listed in Table 12 for ease of reference in the following discussion.

DISCUSSION ON ALARY POLYMORPHISM

Polymorphism was defined by Ford (1956) as 'the occurrence together in the same habitat at the same time of two or more distinct forms of a species in such

Table 12. *The relationship between life-cycle, polymorphism and habitat in* Gerris *and* Velia

	Generations per year	Polymorphism		Habitat
Velia caprai	1	monomorphic apterous		open
V. saulii	1?	monomorphic apterous		open
Gerris najas	1	monomorphic apterous		open
G. costai	1	monomorphic macropterous		closed
G. gibbifer	1	monomorphic macropterous		closed
G. odontogaster	2	summer generation	macropters and micropters	closed
		winter generation	macropterous	
G. argentatus	2	summer generation	macropters and micropters	closed
		winter generation	macropterous	
G. thoracicus	2	summer generation	macropters and sub-macropters	closed
		winter generation	macropterous	
G. paludum	2	summer generation	brachypterous	closed
		winter generation	macropterous	
G. lacustris	2	summer generation	macropters and brachypters	closed
		winter generation	mostly macropters	
G. lateralis	2?	summer generation	macropters and brachypters	closed
		winter generation	mostly macropters	

In all cases where there is a mixed summer generation the numbers of the two forms are about equal. Habitats are described as 'open' or running water, or 'closed', *i.e.* still water habitats only accessible by overland flight. The habitats are fully described elsewhere (Brinkhurst 1959b).

proportions that the rarest of them cannot be maintained merely by recurrent mutation'. This definition allows us to consider all bivoltine species of *Gerris* as polymorphic with the possible exception of *G. paludum*, in which the two generations are alternately long- and short-winged, although the two generations may both be present for a short period. This subject will now be considered under three separate headings:

(*a*) *The occurrence of alary polymorphism*

Poisson (1924) first noticed the increase in the numbers of short-winged forms in the summer, and Mitis (1937) attempted to relate life-cycle and polymorphism.

It has now been established that polymorphism occurs in the summer generation only in most bivoltine *Gerris* species, and both generations in *G. lacustris* and *G. lateralis*. The short-winged forms are the first to appear in the summer populations, suggesting that they are derived from the first eggs laid by overwintered females.

A number of workers have established that polymorphism is commoner in northern latitudes (Sahlberg 1868, Lindberg 1929, Jordan 1943) whilst Teyrovsky (1952) considered both altitude as well as latitude. Ekblom (1941) claimed that short-winged forms were commoner in the winter, but this was based on too short a period of collecting (*see* above). Poisson (1951) described colonies of the usually rare macropterous form of *G. najas* in the Pyrenees, and Hynes (1955) collected more apterous *Tengovelia* and *Microvelia* at high altitudes. Lindberg (1929) noted an increase in the number of macropterous *Gerris najas* in a series of warm summers from 1917 to 1925. An increase in the proportion of long-winged forms would be expected at the limits of distribution of each species owing to migration by flight, and this may account for the unconfirmed abundance of winged *Velia caprai* on the Isle of Man. The widespread occurrence of alary polymorphism in the Heteroptera may well indicate its extreme antiquity in the evolutionary history of the group.

(*b*) *Significance*

Many previous theories of the significance of alary polymorphism have been virtually based on the fact that the mesothorax contains the principal rowing muscles, all the indirect wing muscles, and a proportion of the eggs in fully mature females (Brinkhurst, in press, a). The wing muscles are absent in all short-winged forms and this has led to speculation concerning the utility of the extra space and protein available, although a proportion of this space is lost owing to a slight reduction in size of the thorax. I have shown that, at least in *Gerris lacustris*, there is no difference in the number of eggs in long- and short-winged females, and also that there is no difference in rowing ability (Brinkhurst, in press, a) owing to a greater development of the mesothoracic limb retractors.

Ekblom (1941) kept mixed groups of various polymorphic forms of *G. lateralis* in glass tanks and subjected them to winter conditions, showing that more short-winged than long-winged forms survived and assuming that these conditions held in field populations. Forster (1954) and I have both shown that this is not so, and that there is no change in the proportion of the two forms during the winter. Ekblom (1941) had in fact demonstrated that short-winged forms are more cold-resistant than the long-winged form, this having arisen as an adaptation to field conditions where the macropters (in the two species with a small percentage of short-winged forms in the winter) fly to more favourable overwintering sites far from water, whilst the short-winged forms are forced to shelter close to the summer habitat.

Copulations between long- and short-winged adults show that Poisson (1951) was incorrect in stating that the male genitalia are hypertrophied in the latter,

and Carayon (1944) has shown that the male genitalia of various forms of *Ischnodemus* were identical. The discovery of the short-winged form of *Gerris paludum* and the considerable difference between the male genitalia of this and *G. najas* (Brinkhurst, in press, a) make it certain that at no time were these polymorphic forms of a single species (Poisson 1951).

It seems strange that the inability of short-winged forms to fly should have been neglected in favour of the above theories, but it does appear possible to explain the regular cycle of polymorphism in terms of the need for distribution and overwintering. Monomorphic forms are seen to be apterous on streams where distribution presents no difficulties, the rare macropters probably serving to carry them from one watershed to the next. They are macropterous when inhabiting isolated bodies of water, although the rare flightless forms may serve to maintain them on a suitable habitat from one season to the next. This advantage to the short-winged form would be balanced by selection in favour of macropters when summer conditions dry up many pools and macropters are able to survive. In bivoltine species, the adults fly to overwintering sites and back again in the spring, the second flight constituting the distributive phase, and this generation is entirely or mostly macropterous. Whether or not the short-winged overwintering forms of *G. lacustris* and *G. lateralis* are maintained by selection or are being weeded out of the population will be discussed in the next section, but for the present the only advantage they may conceivably confer on the species is again to maintain it on a particular habitat from one season to the next. They have adapted themselves to winter conditions as indicated above. It is interesting to note that all records of the continental species *G. rufoscutellatus* in Britain are for early spring, a further indication that the post-overwintering flight constitutes the distributive phase (Leston 1956). Many species have been observed on ecologically 'wrong' habitats early in the season, but by May all are in more characteristic habitats (Brinkhurst 1959).

Once the spring populations are well established, the macropters resorb their wing muscles at the same time as they become fully mature, and thus the space and protein available for egg production is increased and flight is prevented at a time when mates must be found. The summer generation is now produced and could be of three types:

(i) A fully winged generation might tend to leave the water whilst the wing muscles were still present and thus leave a food supply, mates and a habitat which has already proved suitable for rearing the young. The flight of these insects is slow, and many may be attacked by predators even if subsequently rejected as unpalatable owing to the scent-gland. Adverse winds, cold, or exhaustion may force them to land, where their only mode of progression is slow and erratic, as the legs are adapted to rowing (Brinkhurst, in press, a). These extra hazards are therefore added to those to which the insects are exposed on the water.

(ii) An entirely flightless generation would remain on the water where predators are few, and would be able to find mates and rear the young on a suitable habitat. The subsequent increase in numbers would lead to severe overcrowding on a small

pond, especially if the habitat deteriorated during the season by drought, pollution of the surface film, or other ecological changes. These disadvantages do not appertain to larger water-bodies, and it should be noticed that the only species inhabiting this situation (*G. paludum*) appears to have an entirely short-winged summer generation.

(iii) A mixture of long- and short-winged forms would provide a non-migratory breeding population coupled with a migratory population which could avoid the increasing population density and deteriorations of the habitat and further the distribution of the species. Therefore, overwintering females producing polymorphic offspring on small, closed habitats, will be at a selective advantage as more of their offspring are likely to survive. It should be stressed that in all instances bar one, selection acts in favour of a mixed summer population, not the short-winged form itself.

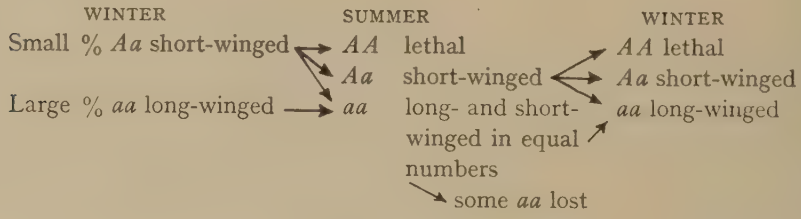
(*c*) *The mechanism of determination*

There are two distinct mechanisms of determination of polymorphism in the Gerroidea, the genetic and the environmental. Poisson (1924) and Ekblom (1941) investigated the genetic aspects of the problem, and I am now able to extend their observations to cover the field situation. It should be noted that both of these authors carried out their experiments on the species which are polymorphic in both generations. Poisson (1924) worked on *Gerris lacustris* and obtained the following type of results (given in outline) whilst Ekblom (1941) obtained a similar picture, using *G. lateralis*.

Expt. 1.	long-winged × long-winged	⟶ long-winged.
Expt. 2.	long-winged × short-winged	⟶ 1 long-winged: > 1 short-winged.
Expt. 3a.	short-winged × short-winged (laboratory specimens)	⟶ 1 long-winged: > 2 short-winged.
Expt. 3b.	short-winged × short-winged (field specimens)	⟶ almost all long-winged, with both long- and short-winged F_1 giving long-winged F_2.

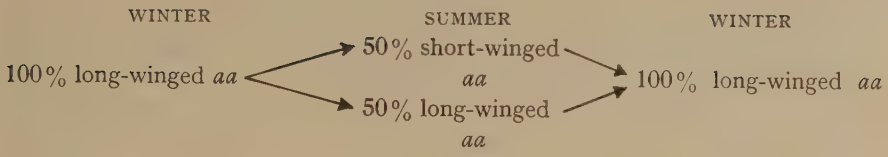
From this, Poisson concluded that a single gene was involved (termed *a* below), such that: *AA* was lethal, *Aa* short-winged, *aa* long-winged. Thus Expt. 1 would be *aa* × *aa*, Expt. 2 would be *Aa* × *aa*, and Expt. 3a *Aa* × *Aa*. He considered that *AA* was lethal as at no time did Expt. 3 give an entirely short-winged generation, but as this genotype is very rare (the short-winged genotype makes up only 10% of the population—see below—therefore the *AA* genotype constitutes only about 0·25% of the population) it is highly unlikely to have been used in these experiments. However, the breeding experiments confirm that the *AA* genotype is lethal or nearly so. From Expt. 2, where there is an excess of short-winged individuals where a 1 : 1 ratio is expected, and even more clearly in Expt. 3b it

will be seen that, owing to environmental factors, some of the short-winged individuals are genetically long-winged (*aa*). The same factors should operate in Expt. 3a so that, if the *AA* homozygote were fully viable, there would be an excess of short-winged forms over and above the expected 1 : 3 ratio. In fact the ratio is of the order of 1 : 2½. If one takes into account that several of the short-winged individuals will be genetically *aa* there can be very few, if any, *AA* individuals represented. Consequently the *AA* genotype must be semi-lethal or lethal. In parallel with other species (*see* below) it is apparent that all the *aa* genotypes are macropterous during the winter when these represent approximately 90% of the population. The remainder, constituting the small percentage of overwintering short-winged forms in *G. lateralis* and *G. lacustris*, are therefore *Aa* genotypes, the breeding data illustrating that whilst the *aa* genotype is polymorphic, the switch only acts in one direction and the heterozygote is always short-winged. The situation is therefore:



This is a balanced situation which has remained stable since at least 1924 and probably for many thousands of generations as the polymorphism is similar on the Continent. Owing to the loss of the *AA* lethals the polymorphism can only be maintained if there is about a 5% selection in favour of the short-winged heterozygote. Although Forster (1954) and I have both indicated that there is no marked difference in the proportions of the two forms before and after overwintering, the slight change in favour of the cold-hardy short-winged form (of the order of 5% in the reduced spring populations) sufficient to give it an overall advantage over the macropters is too small to be detectable in the samples. Another balancing factor could well be the loss of some *aa* long-winged forms in the summer, when migration out of crowded populations adds greatly to the mortality factors normally operating. It is clear that, in these two species, there is selection in favour of a mixed summer generation with a slight net balance of selection for the *Aa* genotype.

Only a small change in the ecology of these species would be required in order to eliminate the *A* gene altogether, and it appears that this has happened in all other bivoltine polymorphic species. In these, the winter generation is entirely macropterous, and therefore entirely *aa* in constitution since micropters cannot become macropters and would be observed in winter populations unless the *A* gene were eliminated. From this we conclude that the environment alone determines the form of the offspring in these species, as it does the majority of individuals in the two discussed above. The situation is therefore:



We have seen from the breeding data that the *aa* genotype may be phenotypically long- or short-winged, and the data on the occurrence and distribution of polymorphism indicates that temperature affects the determination of form. Further, in British *Gerris* species, this acts on the overwintering macropters. Such an alternation of phenotypes with the same genetic constitution is termed an environmental switch mechanism (Mather 1955) and forms one mechanism by which balanced polymorphisms may be maintained (Ford 1945). In *Gammarus duebeni* Lillj. a similar switch mechanism controls sex, operating through the temperature at which vitellogenesis occurs (Kinne 1953). A similar mechanism dependent on winter temperatures may be acting in *Gerris*, where the eggs of overwintered females may be acted upon by cold. The eggs are rudimentary in the autumn, but about half are yolky in the spring, whereas the second batch of eggs mature in the warmer spring months. It is probable that, as the short-winged forms appear first in their generation, they are developed from the first of these egg-batches. This switch mechanism has been operated in the laboratory, using long-winged *G. odontogaster* of the overwintering generation. In the first part of the experiment the insects were collected in the autumn and from five pairs of adults nine long-winged forms were obtained. In the second part of the experiment the same number of adults were collected from the same pond in the following spring, having overwintered in the field, and these gave eight short-winged and twelve long-winged offspring. In both instances adults and eggs were kept at 18-20° C, and nymphs were maintained as near these temperatures as possible. In the first part of the experiment the temperature at which the nymphs were kept sometimes dropped below this level, and in the second part the temperature was higher during a spell of very warm weather. In the field short-winged forms develop earlier in the summer than long-winged forms, and it might therefore be expected that the slightly cooler conditions in the first part of the experiment would encourage the development of short-winged adults and the reverse in the second part, if temperature affected the nymphs. The results show exactly the opposite trend, however, supporting the hypothesis that temperature acts on the gonads of the adult bugs during the winter to produce short-winged adults in the following summer.

It is also instructive to notice that the frequency distribution of the ratio length of hind femur : length of wing bud (used instead of direct measurement of the wing bud to eliminate variations of overall size) indicated that there was no distinction between potential long- and short-winged individuals at this stage. The fate of any individual could only be determined from adults, or older fifth-instar nymphs from which the developing adult could be dissected. At this stage the form of the imaginal wing rudiment is diagnostic, as is the absence of wing

muscles in short-winged forms. This observation would support the view that short-wingedness is a juvenile character produced by a disturbance of hormonal control at the final moult.

The evidence so far indicates that some factor affects the adults during the winter to produce short-winged forms in the subsequent generation. The author feels that this factor is most likely to be low temperatures acting on the eggs at vitellogenesis, the mechanism being a genetic switch of the *aa* genotype manifested through the hormonal control of the final ecdysis. This mechanism is held to operate in all polymorphic *Gerris* species, but in addition there is some genetic segregation involved in determination of wing length of *G. lacustris* and probably *G. lateralis*.

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SUMMARY

1. The life-cycles and alary polymorphism of *Gerris* and *Velia* are described.

2. Univoltine species are monomorphic, stream-dwelling species being apterous, pond-species macropterous.

3. Bivoltine species are polymorphic. The overwintering generation is entirely or largely macropterous, the summer generation mixed in most species.

4. Polymorphic forms are commoner on mountains, in the east of Europe, and in more rigorous climates. Cold seems to be an important determining factor.

5. The significance of the short-winged form lies in its inability to fly. Selection acts in favour of a mixed summer generation in small ponds, and in favour of a short-winged generation in larger water-bodies.

6. Polymorphism is determined by an environmental switch mechanism in all species, with a small degree of genic segregation in *Gerris lacustris* and *G. lateralis*.

7. The genic segregation concerns a single gene, short-wingedness being dominant to long-winged, with the dominant homozygote lethal. The homozygous

recessive form may be expressed phenotypically as long- or short-winged, and is the only genotype in most bivoltine *Gerris* species.

8. The switch mechanism suggested has been operated in laboratory experiments.

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NATURAL MORTALITY OF *ERIOISCHIA BRASSICAE* (BOUCHÉ) (DIPTERA, ANTHOMYIIDAE) DURING THE IMMATURE STAGES OF THE FIRST GENERATION

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(With 1 Figure in the Text)

Recent observations (Wright 1956, 1957, 1958) have shown that certain chemical control measures may increase the infestation of the roots of brassica crops by the larvae of *Erioischia brassicae* (the cabbage root fly). This work led to the conclusion that the insecticides were interfering with a system of natural control of the larval population. To aid the interpretation of these results detailed investigations of the population dynamics of *E. brassicae* were begun in 1955, together with studies of the biology and habits of associated parasites and possible predators.

There are many references in the literature to organisms responsible for mortality at different stages in the development of *E. brassicae*. Predation of the egg stage by trombidiid mites (Schoene 1916, Gibson & Treherne 1916, and Lowry 1915), ants (Schoene 1916) and by carabid and staphylinid beetles (Wishart, Colhoun & Monteith 1957) has been recorded. The last team of workers stained eggs with a solution of Bengal rose and placed groups of marked eggs around plants in the field. Collections made after periods of 24, 48 and 72 hours showed large daily losses of marked eggs. Mortality in the larval stage has been caused by predatory ants (Schoene 1916), beetles (Gibson & Treherne 1916, de Wilde 1947) and other anthomyiid larvae (Smith 1927). Many hymenopterous parasites attack the larval stages but the mortality occurs after the puparium is formed. Five species of the Braconidae, three of the Cynipidae, and four of the Ichneumonidae, have been reared from *E. brassicae* puparia (Wadsworth 1915, James 1928, Paillot 1914, Schoene 1916, Vodinskaya 1928, Colhoun 1953, de Wilde 1947, Nixon 1939, and Wishart, Colhoun & Monteith 1957). Of these parasites only the cynipid *Idiomorpha rapae* (Westwood) is of major importance. Parasitism of the pupal stage by species of *Aleochara* (Coleoptera, Staphylinidae) has been recorded by most of the authors cited above. Predation of the adult flies by anthomyiids (Schoene 1916) and by cordylurids (Hobby 1931, Reid 1958) has been recorded. The adult stage is also attacked by the entomogenous fungus, *Empusa musca* (Schoene 1916).

Various techniques have been developed to estimate the populations of the immature stages of *Erioischia brassicae*, and while the present paper deals only with the population dynamics of the first generation, the same techniques have also been used in investigations of the later generations of the life-cycle. The

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analyses of the mortality in other generations will be the subject of later papers to which the present paper is partly an introduction. The object of all these investigations is to make a quantitative comparison of the importance of each mortality factor as a control of the population of *E. brassicae* from year to year.

THE BIOLOGY OF *ERIOISCHIA BRASSICAE*

Certain details of the biology, life history and physiology of *Erioischia brassicae* are essential to a critical appraisal of the sampling methods used to estimate population changes and also to the interpretation of these changes in terms of natural mortality. The key features are indicated in the following brief account of observations on *E. brassicae* made at Wellesbourne.

The species usually passes through three generations during the summer and overwinters in the diapausing pupal stage. A diapause occurs in all third-generation puparia and sometimes in those of the second generation. The first generation, which forms the subject of this paper, begins with the eggs laid by flies which have emerged from the overwintering puparia. Unless the season is very early these flies appear during the second half of April. Each female fly lays up to eighty eggs during the first 2 or 3 weeks of life and if the fly survives longer a second batch of eggs may be laid. The eggs are normally laid singly, and the fly moves from plant to plant laying only a few eggs around each. The first eggs appear in the soil around the host plant at the beginning of May, but cold weather may delay the main oviposition period for another week or more (Miles 1954). Once settled warm weather occurs the combination of large numbers of flies and their method of oviposition adds a fairly uniform number of eggs to each plant every day for the next 3 weeks, only severe weather causing much variation. Once the peak oviposition period has passed the number of eggs laid per plant per day becomes low and irregular, probably representing the second batches of eggs of the surviving flies.

The eggs are normally laid in the soil within a distance of about 5 cm around the stem of the host plant; favoured oviposition sites are soil crevices or on the underside of soil crumbs. The eggs are shining white in colour and just under 1 mm long and 0·3 mm broad, the whole being slightly curved. The eggs are differentiated from others found in the soil by their size, colouring and by the characteristic sculpturing on the chorion (Smith 1927, Miles 1952). The incubation period of the eggs depends on the temperature and varies between 2 and 14 days (de Wilde 1947). Calculations based on de Wilde's data indicate a temperature threshold of development at 7·2 C. This threshold has been confirmed by us in further experiments, and it has been shown that about 96 day-degrees above 7·2 C are required to complete the development of the eggs to hatching.

The first stage larvae hatch from the eggs and make their way down to the root system of the host plant where they begin to mine the root cortex. The later larval stages confine their activities to the larger roots. There are three larval instars, all white and conical in shape. They can be differentiated from other

larvae present around the root systems by the shape of the cephalopharyngeal skeleton, the spiracles and the pair of bifid tubercles at the posterior end (Miles 1952). The first instar feeds for about 4 days before moulting, the second for about 6 days and the third stage may feed for 10-20 days before completing its development. The greatest numbers of larvae are present on the roots of the host plants during May and June.

At the end of the third larval stage the individuals migrate from the roots into the surrounding soil to pupate. The distance travelled before pupation occurs seems to depend on the extent of the root system of the plant and on the soil moisture conditions. Most of the larvae feeding on the compact root system of cabbage pupate within 5 cm of the main root, but on cauliflowers 15-20 cm is by no means unusual. Pupation of the early larvae starts at the beginning of June and the bulk of the larvae reach this stage before the middle of July. The puparium is formed from the last larval skin and retains the characteristic larval mouthparts and the bifid anal tubercles. The puparia vary in size up to 8 mm long and 3 mm broad. Much smaller specimens occur, which are frequently found to be parasitized by *Idiomorpha rapae* (Westwood) Hymenoptera, Cynipidae. Such parasitized pupae often have small black spots of meconium towards one end.

A diapause does not normally occur in first-generation pupae, and the adults emerge from them within about 20 days of the start of the instar. The main bulk of the adults emerge in the field during late June and most of July. Adults of *Erioischia brassicae* are about 7 mm long, the males dark grey and bristly, the females a lighter buff grey with fewer bristles (Smith 1927).

METHODS OF ESTIMATING THE POPULATIONS OF THE DIFFERENT STAGES

(*a*) *The egg stage*

The eggs and empty chorions float on water, and this provides a ready method of recovering the eggs from soil in which they have been laid. To determine the numbers present, the soil within 5 cm of the host plant stem is carefully removed with a spoon to a depth of 2 cm and is then stirred into a dish of water. The soil falls to the bottom leaving the eggs floating in the surface scum where their whiteness makes them apparent. They can be removed with a fine paint brush and placed on black filter paper for examination and counting. The population of eggs found around a plant by this method will be an accumulation of all those recently laid, together with the empty chorions of the older eggs which have already hatched.

When the soil containing the eggs is removed from around the plants fresh soil is replaced to bring the site back to normal. By making a second count of the eggs in this fresh soil after a given period, the number of eggs laid during that time is obtained. Consecutive egg counts from groups of similar plants give an estimate

of the total number of eggs laid per plant over a long period. The scheme of egg counting is given below.

Day	Soil cleared and replaced	Eggs counted and soil replaced
1	Plants (A)	
2		
3		Plants (A) ...E3
4		
5	Plants (B)	Plants (A) ...E5
6		
7		Plants (B) ...E7
8		
9	Plants (C)	Plants (B) ...E9
Etc. . . .		

The sum of the egg counts E3+E5+E7, etc., gives the estimated total of eggs laid from day 1 onwards. Egg counts from ten randomly selected plants have been found sufficient for good estimates to be made of the number of eggs laid on crops of cultivated host plants. By making the intervals between the counts short, hatched eggs will not normally occur. During cool weather, longer periods than 2 days can be left between the egg counts. The demonstration of egg losses caused by predation, Wishart *et al.* (1957), shows the limitations of this egg counting technique. The counts made will represent the total number of eggs laid, less the number lost through predation. A modification of Wishart's technique of demonstrating egg losses was used to show that in 1958 substantial losses of marked eggs (30-50%/day) also occurred at Wellesbourne. Therefore it is likely that all the egg counts made underestimate the actual number of eggs laid.

(*b*) *The larval and pupal stages*

The numbers of larvae and pupae around the plants are estimated by taking a sample group of ten soil cores each containing the main root system of one plant. The larvae and puparia are separated from the soil by a brine flotation technique. The soil is washed through a coarse sieve (3 meshes/cm) into a fine sieve (32 meshes/cm). Puparia and large larvae may be retained in the coarse sieve and are collected from it. The fine sieve is then partly sunk into a brine tank and brine is forced up through it, overflowing through a lip into another fine sieve (16 meshes/cm). In this way the organic material is collected into this final sieve, from which the larvae and puparia are separated by picking over the debris, small portions of which are spread out in dishes of water. When the adult flies emerge, the puparia are usually left intact and if not waterlogged or broken up they will appear among the debris with the full puparia.

For accurate determination of the numbers of each larval instar in a sample, a biometric method has been developed to facilitate identification. The larvae are

cleared in warm caustic potash (10%) and transferred to glycerine, on a slide. The distance between the tip of the mandible and the posterior end of the ventral process of the pharyngeal sclerite is measured, as indicated in Fig. 1. The measurements fall into three distinct groupings with means of 0·29, 0·53 and 0·88 mm, corresponding to the 1st, 2nd and 3rd stage larvae respectively. A large series of measurements is summarized in the histograms of Fig. 1.

Investigations have been made into the distribution of the puparia around the

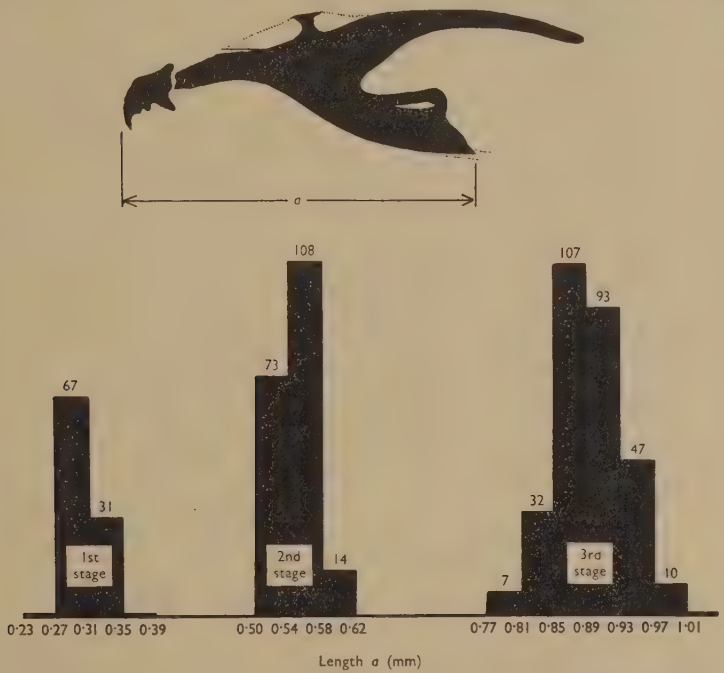

Fig. 1. Separation of the larval instars of *Erioischia brassicae* by biometry of the bucco-pharyngeal armature.

host plant in 1957 and 1958. Large numbers of small soil cores taken at different distances from the cabbage stem have shown that in both years 93% of the puparia would be collected in the 15 cm diameter soil cores used in the present study. The numbers of puparia in the samples have therefore to be corrected by a factor of 1·08 to make them comparable with the larval numbers in similar samples.

(c) *Newly emerged adults*

Two methods are available to count the number of adult flies emerging from the pupal population. The pupae from the soil samples can be reared in gauze-topped jars in the insectary, and the proportion of adult flies to parasites, etc., can be observed. Since the flies always emerge before the parasites in the field the empty

puparia will mostly represent the former. Thus the empty puparia must be counted as emerged flies to avoid a biased measurement of parasitism. In this way all the samples of puparia taken from the field before the parasites began to emerge, as observed in a cool insectary, can be used to provide several estimates of the proportion of emerged adults.

The second method is to place collecting cages over the host plants at the appropriate time and to count the emerged flies. To obtain normal emergence the collecting cage should interfere as little as possible with the growth of the host plant. Transparent plastic netting (5 meshes/cm) has been found suitable material for these cages; those in use at Wellesbourne are in the form of a 50 cm cube, open

Table 1. *The larval and pupal populations of samples of ten plants, first generation 1958*

Sampling date	1st larvae	2nd larvae	3rd larvae	Puparia	Puparia ×1·08
8 May	0	0	0	0	–
12 May	20	3	0	0	–
15 May	19	18	0	0	–
19 May	36	40	3	0	–
22 May	8	31	21	0	–
27 May	34	74	58	0	–
30 May	24	83	120	0	–
2 June	22	57	143	2	2
5 June	37	94	95	22	24
9 June	11	52	152	43	46
13 June	16	49	99	64	69
19 June	6	31	111	110	144
25 June	3	16	88	167	180
3 July	0	7	43	169	182
10 July	0	2	9	168	181
17 July	2	9	12	248	268
25 July	0	0	5	228	246
31 July	3	8	21	187	202
8 Aug.	0	1	5	259	280
14 Aug.	0	2	6	203	219

at the base. The flies are removed through a muslin side sleeve. Ten of these cages are moved to cover a new group of randomly selected plants every few days. Newly emerged flies are collected each morning.

POPULATION ESTIMATES

The above methods have been used over the years 1954-8 to study the numbers of the immature stages of the first generation of *Erioischia brassicae*. The 1954 records were made on the population of a cauliflower crop, but subsequently all records have been made on a cabbage crop. No field records of adult emergence were made until 1957. As typical examples of the records obtained, Table 1 shows the detailed soil sampling results for the 1958 generation on one crop of summer cabbage, while Table 2 compares the running total of 2-day egg counts with the build-up of the numbers of the later instars. The build-up of the numbers of the larval instars is derived from Table 1, for example on 5 June, the presence in the

sample of 37 first, 94 second, 95 third stage larvae together with 24 puparia indicates that a total of 250 individuals have reached the first instar, 213 individuals the second instar and 119 the third instar. The puparia numbers in Table 2 are

Table 2. *The build-up of the number of individuals which have reached each instar, compared with the number of eggs laid and the number of adults emerging (samples of ten plants)*

Sampling date (i)	Eggs laid (ii)	1st larvae (iii)	2nd larvae (iv)	3rd larvae (v)	Puparia (vi)	Adults emerged (vii)	Reared adults (%) (viii)
8 May	eggs added at rate of 5-10 per week	0	0	0	0	0	–
12 May		23	3	0	0	0	–
15 May		37	18	0	0	0	–
19 May		79	43	3	0	0	–
22 May		60	52	21	0	0	–
27 May		166	132	58	0	0	–
30 May		227	203	120	0	0	–
2 June		224	202	145	2	0	–
5 June		250	213	119	24	0	46
9 June		261	250	198	46	0	–
13 June		233*	217	168	69	0	70
19 June		258*	252*	221	110	0	46
25 June		287*	284*	268	180	2	40
3 July		232*	232*	225*	182	19	60
10 July		192*	192*	190*	181	56	53
17 July		291*	289*	280*	268	62	54
25 July		251*	251*	251*	246*	68	49
31 July		234*	231*	223*	202	96	–
8 Aug.		286*	286*	285*	280*	110	–
14 Aug.		227*	227*	225*	219*	119	–
Peak numbers	2200	250	249	240	248	127	Mean 52

* Data used to calculate the peak numbers.

identical with those of the last column of Table 1. The running total of the field emergence of adults is also given for comparison with the build-up of the immature stages. The final column of Table 2 shows the percentage of adults reared from the

Table 3. *First generation 1954-8: population estimates (average numbers per plant) and losses between stages (%) in parentheses*

	Eggs	Larvae	Puparia	Adults
1954	460 (93·1)	40 (10·0)	36 (70)*	–
1955	160 (98·5)	3+ (0)	3– (69)*	–
1956	94 (75·5)	23 (1·0)	23 (48)*	–
1957	190 (79·8)	39 (27·0)	28 (66)†	10
1958	175 (85·4)	25+ (2·0)	25– (49)‡	13

* Data obtained by rearing puparia in an insectary.
† 65% in insectary.
‡ 48% in insectary.

puparia contained in each sample. The peak numbers of the larval instars and the puparia are estimated from the average accumulated population of those samples (indicated by an asterisk in the table) where earlier instars form less than 5% of

the total sample population. Similar population estimates made during the first generations over a period of 5 years are summarized in Table 3, where the differences between the numbers of successive stages are expressed as percentage losses. As pointed out already, the total number of eggs laid is underestimated in every case and this will result, therefore, in the underestimation of the losses between the egg and larval stages shown in Table 3.

The data of Table 3 are sufficient to show that in every year the major losses occurred between the egg and larval stages and between the pupal and adult stages. The possible causes of mortality during the development of *E. brassicae*

Table 4. *Possible causes of mortality during the immature stages of* Erioischia brassicae *suggested by observations made at Wellesbourne*

Age interval		Possible causes of mortality	Referred to in Table 3 as losses between:
Egg stage	(*a*)	Reduced viability	Egg and larval stages
	(*b*)	Egg losses, predation, etc.	
Newly hatched larvae	(*c*)	Adverse weather at hatching	
	(*d*)	Failure to find host plant	
First larvae, Second larvae, Third larvae	(*e*)	Mortality caused by the death of host plant	Larval and pupal stages
	(*f*)	Losses caused by predation, etc.	
Pupal stage	(*g*)	Parasitized by: *Idiomorpha rapae, Phygadeuon trichops, Aleochara* spp.	Pupal and adult stages
	(*h*)	Other causes of failure to emerge, disease, etc.	
	(*i*)	Puparia losses, predation, etc.	
Newly emerged adults	(*j*)	Failure to reach soil surface	

are set out in Table 4, classified into those affecting each age interval of the generation.

DISCUSSION

These preliminary investigations of the natural mortality in the first generation show that on the average more than 95% of the individuals died during development. In attempting to assess the importance of each of the mortality factors operating during the first generation the comprehensive discussion of the interpretation of insect mortality data given by Morris (1957) has been a useful guide. His main points are: that in explaining changes in population from year to year and place to place the importance of a mortality factor depends on its capacity to vary the proportion of individuals which survive each generation; that a mortality factor causing a constant proportion of deaths cannot itself cause variations of survival from generation to generation; and that a variable mortality, on the other hand, will cause the survival to vary. The importance of the variability of a factor depends on the magnitude of the change of survival it causes. Bess (1945) shows how the variations in high mortalities have a greater effect on the surviving population numbers than variations in low mortalities. For example, in a population where 99 individuals out of 100 die, a variation of one death either way makes

a 100% difference, whereas the same variation in a population where only 10 individuals out of 100 die would hardly be noticed. Furthermore, in the effect of variations it is immaterial whether the high mortality results from one factor or several factors acting contemporaneously. Reverting to the example given, changes in the 10% mortality would become just as important as changes in the 99% mortality if the former was contemporary with 89% mortality caused by other factors.

In the *Erioischia brassicae* data for 1954-8 (Table 3) probably all the factors vary sufficiently to cause alterations of the proportion of individuals surviving each generation. The three immature stages have different levels of total contemporary mortality, the highest occurring during the egg stage, the next highest during the pupal stage and the lowest in the larval stage. Therefore variations in these mortalities will vary in importance in that order. The quantitative importance of the variations observed in the mortalities of the first generations of *E. brassicae* over the whole period 1954 to 1958 can be judged by using an index of population trend of the type used by Balch & Bird (1944). This index can be defined as the

Table 5. *The relative importance of the mortalities during the first generations, 1954-8*

Mortality occurring during:	Average survival (%)	Greatest survival (%) a	Least survival (%) b	Index of population trend (average survival = 100) a	b
Egg stage	15	25 (1956)	2 (1955)	167	8
Larval stage	92	100 (1955)	74 (1957)	109	83
Pupal stage	37	52 (1956)	30 (1954)	140	81

percentage change from the average survival during a particular stage, the average survival being taken as 100%. Table 5 shows the effect on the index of the largest recorded variations of the mortality occurring during the egg, larval and pupal stages. The index of population trend shows how in 1956 the egg mortality was so low that there was a 67% increase in larval numbers, while in 1955 this mortality was so high that there was a 92% decrease in larval numbers. Comparison with the mortalities of the other stages shows the egg mortalities to be the main controlling factors of this generation. Their importance is enhanced by the fact that the egg mortalities are known to be underestimated, the higher level of average mortality accentuating the effect of the variations of the mortality on surviving population numbers.

A final point made by Morris is that survival changes resulting from the variation of a particular mortality may be affected by the sequence in which any density-dependent and density-independent factors operate. The only clear case of a density-dependent mortality in the present study is the mortality caused by the death of host plants. Decreases of the egg mortality which give rise to large numbers of first-stage larvae are balanced by the inability of the host plant to support this larger population. This effect can be seen in the data for 1957 (Table

3) where the large numbers of small larvae combined with the effects of a dry spring to cause 34% deaths among the host plants. Consequently the numbers of later larvae and pupae were considerably reduced.

The accuracy of the assessment of the importance of the egg mortality in the population dynamics of the first generation of *E. brassicae* is limited by the shortcomings of the egg counting technique. Further study of the egg mortality will require an estimate of the actual total number of eggs laid, which in turn will require a day-to-day measure of the naturally occurring egg predation. These problems will be dealt with in another paper.

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SUMMARY

1. A brief account is given of the biology of *Erioischia brassicae*.

2. Methods are described for the enumeration of the populations of the different stages of the life-cycle.

3. Five years' records of the population losses occurring during the first generation are summarized, and possible causes of mortality are listed.

4. Discussion of the mortalities occurring during each stage of the life-cycle suggests that the egg mortalities are the most important.

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THE COOLING WATER OF POWER STATIONS: A NEW FACTOR IN THE ENVIRONMENT OF MARINE AND FRESH-WATER INVERTEBRATES

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(With 2 Figures in the Text)

Modern industry brings many new factors into the natural environment, which may be expected to affect the natural balance. Although the literature regarding many such factors is abundant, it seems that the problems connected with the effect of power station discharges and how aquatic organisms respond to them are still largely a matter for speculation (see, however, Van Vliet 1957). A wide field is open for biological investigations on the response of aquatic organisms to these new factors.

The increasing demand of modern industry for electric power brings every year more power stations on the rivers and by the sea. Cooling water, either from the sea or from the river, is essential for running them. In 1957 about 76 000 million units of electricity were supplied in England and Wales by the Central Electricity Authority. Nearly all of this, together with current generated for its own use, was generated in thermal plant (steam turbine and diesel engines) and required an estimated 4×10^{12} gallons ($18{\cdot}2 \times 10^{12}$ litres) of cooling water. Very approximately, a third of this was river water, a third sea water or brackish estuarine water, and a third water that had been recirculated over cooling towers: of the latter, about 3% on average would be fresh make-up water and about 2% returned to the water course, the 1% difference being evaporated. All this water contains living organisms, if only bacteria and fungi.

It is intended in this paper to give a general picture of the conditions created by power stations in freshwater and marine environments and some information on the animal species involved and their response to the conditions they experience.

MATERIAL AND METHODS

The material for this investigation was collected in the years 1955-7 in the intake and outfall water of the twelve power stations listed in Table 1. Fig. 1 shows their geographical distribution. The year 1955 was spent on exploration to find out the most suitable places for collecting material: that is to say where the conditions created by the power stations are altered as little as possible by other industrial disturbances. As a result, three power stations were selected for detailed study, namely: Leicester and Wakefield 'B', using fresh water for cooling purposes, and Roosecote, taking water from a brackish dock connected with the sea. The two following years, 1956 and 1957, were mainly spent at these stations. The information from the other nine stations served as useful background data,

particularly regarding the distribution of fauna for different parts of the country.

Roosecote and Wakefield 'B' are the most modern of the power stations surveyed. The former started operating on 25 September 1953, and Wakefield 'B' on 23 December 1955. Leicester, though much older, has been operating as it is now since 17 December 1949 after being modernized. This station has some generating sets cooled directly by river water, and some sets cooled by means of water from the same river which is recirculated through cooling towers.

Table 1. *List of the power stations surveyed*

Name of the power station	Locality	Date of survey	Character of water
Carlisle	River Caldew	24 May 1956	fresh water
Ironbridge	River Severn	15 September 1955	,, ,,
Leicester	River Soar	16 August 1955	,, ,,
		26 June 1956	,, ,,
		9 July 1957	,, ,,
		27-29 August 1957	,, ,,
Wakefield 'B'	River Calder	18 August 1955	,, ,,
		6 October 1955	,, ,,
		27 June 1956	,, ,,
		25 September 1956	,, ,,
		20 August 1957	,, ,,
Worcester	River Severn	14 September 1955	,, ,,
Carmarthen Bay	River Loughor	13 September 1955	estuarine
		31 July 1956	,,
East Yelland	River Taw	17 October 1955	,,
		8-9 August 1956	,,
Plymouth	River Plym	14 October 1955	,,
		21 August 1956	,,
Brighton 'B'	Shoreham Harbour	8 September 1955	sea water
Poole	Holes Bay	2 September 1955	,, ,,
		15-16 May 1956	,, ,,
		3 September 1956	,, ,,
		9 April 1957	,, ,,
Portsmouth	Portsmouth Harbour (Camber Dock)	10 October 1955	,, ,,
Roosecote	Morecambe Bay (Cavendish Dock)	11 August 1955	sea and brackish water
		11 September 1956	,, ,,
		19 June 1957	,, ,,
		11 February to 31 September 1957	,, ,,

Material has been collected from the inflowing and outflowing cooling water for both qualitative and quantitative studies. The qualitative samples were collected by means of a nylon phyto-plankton net of 180 meshes per inch (74/cm). This net was placed in the intake and outfall and kept there for 20 min, allowing the water to pass through. The plankton organisms stopped by the net were drained into glass containers and immediately examined under the microscope in the station chemical laboratory. After a preliminary examination of the living material the samples were fixed for more detailed examination, using 4% formaldehyde for freshwaterorganisms and 5% for marine forms.

The velocity of the water is usually higher at the outfall than at the inlet, and so this simple method of collection could not be used for quantitative comparisons. For this purpose a pump and a 10 l. plastic bucket were used, the water being percolated through the same kind of net supported in a vertical position on the bank. For one sample the bucket was filled five times and the organisms in the

Fig. 1. Geographical distribution of power stations surveyed.

50 l. of water were concentrated into 25 ml samples and fixed in formaldehyde for examination. Ten such samples were obtained at each place, so that, in all, the organisms from 500 l. of water were made available.

Because of the turbulence created by the power station suction some representatives of benthos were found in the samples with the plankton. In order to have a general picture regarding benthos, a number of samples of bottom fauna were

Table 2. *Physical and chemical properties of fresh water used for cooling purposes*

Power station	Date of survey	Inlet water: Time of day	Inlet water: Temp. °F	Inlet water: Temp. °C	Inlet water: pH	Inlet water: Dissolved oxygen (p.p.m.)	Inlet water: Dissolved oxygen Satn (%)	Outlet water: Time of day	Outlet water: Temp. °F	Outlet water: Temp. °C	Outlet water: pH	Outlet water: Dissolved oxygen (p.p.m.)	Outlet water: Dissolved oxygen Satn (%)	Outlet water: Chlorine residual (p.p.m.)	Outlet water: Rate of flow gal/h $\times 10^6$	Outlet water: Rate of flow l./h $\times 10^6$
Leicester.																
open system	26 June 1956	a.m.	73	22·8	8·0	6·2	74	p.m.	88·3	31·3	8·0	6·6	90	–	1·35	6·1
Leicester:																
closed system	29 August 1957	p.m.	72	22·2	8·4	8·4	99	a.m.	84·6	29·2	8·4	8·1	106	< 0·1	3·1	14·1
Wakefield 'B'	27 June 1956	p.m.	68	20·0	7·2	4·4	50	p.m.	76·2	24·6	7·2	5·6	69	0	2·6	11·8
Wakefield 'B'	25 September 1956	a.m.	63·5	17·5	6·8	6·2	67	p.m.	77	25·0	6·6	7·1	87	–		
								p.m.	76	24·4	6·8	7·0	86	0·2	2·6	11·8
Wakefield 'B'	20 August 1957	a.m.	65	18·3	6·8	2·9	32	p.m.	78	25·5	6·8	4·8	60	0	10·4	47·3

Table 3. *Physical and chemical data found in sea water used for cooling purposes*

		Inlet water							Outlet water								
Power station	Date of survey	Time	Salinity (‰)	Temp. °F	Temp. °C	pH	Dissolved oxygen (p.p.m.)	Dissolved oxygen Satn (%)	Time	Salinity (‰)	Temp. °F	Temp. °C	pH	Dissolved oxygen (p.p.m.)	Dissolved oxygen Satn (%)	Chlorine residual (p.p.m.)	Rate of flow gal/h $\times 10^6$	Rate of flow l./h $\times 10^6$
Brighton 'B'	8 September 1955	a.m.		68·5	20·3				a.m.		79	26·1				0·65		
Carmarthen Bay	31 July 1956	p.m.	31·6	61·9	16·6	8·0	7·8	100	p.m.	31·6	72	22·2	8·0	7·9	111	0·15	12	54·5
East Yelland	17 October 1955										57·5	14·2				0·6-0·9		
East Yelland	9 August 1956	p.m.	32·5	65	18·3	7·5	9·8	130	a.m.	32·5	75	23·9	8·0	8·3	124	0·25	3	13·6
Plymouth	14 October 1955										70	21·1				0·3		
Plymouth	21 August 1956	a.m.	31	67	19·4	8·0	7·0	95	p.m.	31	62·5	16·9	8·0	7·3	93	0·3-0·4	4·8	21·8
Poole	2 September 1955			70	21·1						88	31·1				0·5	8	36·4
	15 May 1956	a.m.	29	58	14·4	7·7	8·1	98	p.m.	29	75	23·9	7·9	8·2	117	0·3		
	16 May 1956	a.m.		59	15·0	7·8	7·3	89	p.m.		76	24·4	7·8	7·7	111	0·3		
	3 September 1956	a.m.	28·6	59	15·0	8·1	7·9	96	p.m.	26·9	75	23·9	8·0	7·9	111	0·2-0·55		
	9 April 1957	a.m.	26·9	48	8·8	8·1	9·3	98										
Roosecote	11 August 1955		25	71	21·7					25	84	28·8						
	11 September 1956	p.m.	13	62·5	16·9	8·1	8·5	97	p.m.	13	73·8	23·2	8·1	8·2	106		40	181·8
	19 June 1957								a.m.	7·8	74·8	23·8	8·1	8·3	105	< 0·1		

collected with the dredge at Roosecote, both from the area washed over by the outfall water and from unaffected areas. The dredge was also used in the cooling tower ponds at Leicester and the handle net at Wakefield 'B' power station. During the collection of zooplankton and bottom fauna, information on the water temperatures at the intake and outfall, and on the pH, salinity, dissolved oxygen content and chlorine residual of the water was also obtained. The pH was determined with a glass-electrode pH meter except at Leicester where a colorimetric method was used. Dissolved oxygen was determined by Alsterberg's modification of Winkler's method and the percentage saturation calculated from Truesdale, Downing and Lowden's (1955) figures: residual chlorine was determined in accordance with the methods recommended by the Ministry of Housing and Local Government (1949) for sewage analysis. Typical results obtained by the chemist of the C.E.G.B. Biological Laboratory, Miss E. Evans, are shown in Tables 2 and 3.

THE USE OF WATER FOR COOLING AND ITS EFFECTS

(*a*) *The cooling water*

In order to have a better understanding of the changes caused by power stations and their possible effect on aquatic organisms, a brief description of the water

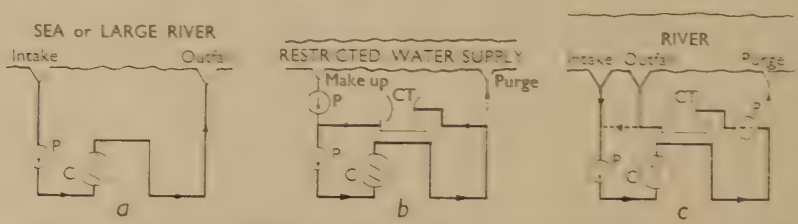

Fig. 2. Diagram showing three systems of cooling water circulation in power stations. *a*, open system; *b*, closed system; *c*, mixed system. P, pump; C, condenser; CT, cooling tower. The broken line shows the alternative scheme of the mixed system.

circulation in the plant is essential. Three types of cooling water system can be distinguished as shown in Fig. 2. In the open or direct system, water is drawn into the plant from the sea, river or estuary through coarse screens which exclude large floating debris such as logs, and then through band screens with a mesh of $\frac{3}{8}$ in. (9·5 mm). It then usually passes through pumps to the condensers, which are composed of a number of tubes, usually brass, 1-1$\frac{1}{4}$ in. (25-32 mm) in diameter. These tubes are commonly about 17 ft (5·2 m) long and arranged in two banks so that the water flows through one bank, into a turn header box, and back through the other bank. The water is then discharged back to the sea or river through the outfall culvert. In some stations, *e.g.* Roosecote, there are three passes in the condenser. At Roosecote there are over 2000 tubes in each of the three sections of one condenser, the water velocity being 6·2 ft (1·9 m) sec. The rate of flow is 1$\frac{1}{4}$ million gallons ($5{\cdot}68 \times 10^6$ l.) of water per hour for each condenser. The rise of temperature through the condenser is between 10 and 15° F (5·5-8·5° C): Roosecote

produces a rather greater temperature rise than is common elsewhere because of the three passes through the condenser instead of two. The rise of temperature does not depend on the season of the year, but it will increase if the cooling system becomes inefficient by reason of growths of bacterial or fungal slime on the tube surfaces. To prevent the growth of any such film the water at the condenser inlet is normally treated intermittently with chlorine. In modern plants quite high doses of chlorine are applied for short periods of perhaps 5 min to each condenser in turn, the dose being repeated every 3 hours or less frequently. In some older plants several condensers are treated at once with a smaller chlorine dose, which has to be maintained for a longer time, perhaps 20 min, to be effective. In some cases also, sodium hypochlorite is used instead of chlorine. Many power stations using sea water have a continuous or intermittent application of chlorine at the beginning of the intake culvert to prevent the settlement and growth of mussels, and this serves also to keep the condensers free from slime.

When only a limited quantity of water is available it can be cooled in cooling towers and recirculated in a closed system. Cooling towers are of several types. The most conspicuous are the huge hyperbolic towers now generally employed by the electrical industry in this country. These shells may be 300 ft (91·4 m) or more high and over 100 ft (30·4 m) in diameter at the base. For the most part they are just chimneys to create a draught of air. In another type of tower this draught of air is caused by a large fan in the top of the tower, and such towers are not nearly so high. In either type, the bottom 30 ft (9·14 m) or so consists of wooden laths or louvres over which water is sprayed. As the water drips from lath to lath it comes into intimate contact with the upflowing draught of air and is cooled. It is collected in a pond at the base of a tower and recirculated through the condenser. At Leicester power station the cooling ponds associated with part of the generating plant have a capacity of 320 000 gallons ($1{\cdot}45 \times 10^6$ l.), and the water goes round the system between four and five times an hour. The water cools by evaporation and about 1 % is lost on each passage through the tower. This loss must be made good by means of a make-up of fresh water, and in order to keep down the concentration of salts there must be a bleed-off or purge back to the river. Where the water is good quality but is expensive or the supply is restricted, the purge is kept to an absolute minimum so that the make-up is small. At Leicester, where some of the generating plant is operated direct from the river on the open system, there is plenty of water for the cooling tower system and the make-up is high, so that the water in the cooling tower system is constantly changing.

At Leicester an open system and a nominally closed system are operated side by side. On the other hand, at Wakefield the towers are used in conjunction with the river to supplement the flow when the river is low. This system is known as a mixed system.

(*b*) *Factors introduced by the use of water for cooling*

The use of water for cooling by a power station introduces new factors into the environment of the aquatic organisms. The principal changes are: the increase of

pressure caused by the pumps; the rise in temperature; the injection of chlorine; turbulence in the pumps, at the entrance to the condenser tubes and in the discharge culvert; and the break up of the water into a heavy rain if it is passed through cooling towers.

The physical conditions to which the water is subjected at Wakefield 'B' may be regarded as typical. The water is drawn from the River Calder, which in late summer carries a flow of $4{\cdot}6 \times 10^6$ gal ($18{\cdot}27 \times 10^6$ l.) h at a velocity of about 0·7 ft (0·2 m) sec. The water passes through the screens and enters the pump under suction. The action of the pump blades increases the velocity to something over 40 ft (12 m) sec, and this energy is converted into a pressure that amounts to about 1·6 atmospheres absolute. The water is forced up to the condensers and through the tubes at a velocity of 6-7 ft (1·8-2·1 m) sec, and emerges at a reduced pressure. Since the condensers are situated well above the level of the water in the river to avoid the danger of flooding the plant, the syphonic suction head of the return duct back to the river is made use of, and the water at the condenser outlet is actually under a reduced pressure about $\frac{1}{2}$ atm absolute. If the cooling towers are in use, some of this water is drawn through a second set of pumps capable of forcing it through sprays 30 ft (9·14 m) from the ground, so a pressure of 2 atm or so is generated. The organisms in the water thus suffer pressure changes over a 4 to 1 range, and velocities, with accompanying turbulence, up to about 40 ft (12 m) sec, over the period of about 3 min during which they are passing through the plant.

The temperature rise is confined to the condenser tubes. In a typical two-pass condenser there is a smooth rise of approximately 7° F (4 C) during passage through one tube, which takes about 3 sec, then a short pause in the return header box, followed by a further rise of 6 or 7° F (3-4° C) in the tubes in the second pass. Sometimes the difference between the outfall temperature and that of the natural river shows greater temperature rise than this, but this is due to recirculation of the same water through the system. This phenomenon occurs in open systems when the flow through the condensers exceeds the flow in the river, and it can also occur in closed systems when the air temperature is high. In a cooling tower system the warmer the water entering the cooling tower the more it cools. On a warm day the temperature has to build up gradually to the point at which the range of cooling in the tower becomes equal to the range of heating in the condensers. In a closed cooling tower system, therefore, the temperature level in the system can be almost independent of the temperature of the make-up water drawn from the river. The organisms entering with the make-up water are subject to stepwise increases of temperature as they are mixed with the recooled water and then passed through the condenser, but the organisms inhabiting the cooling tower pond suffer only a gradual temperature increase, which usually reaches a maximum in the early afternoon.

In power stations operating on fresh water or on sea or estuarine water where mussels are not a problem, chlorine is injected close to the condensers, usually as a strong aqueous solution prepared in a chlorinating plant. The chlorine is injected into only a fraction of the total water flow at one time, usually that

flowing through one condenser or one half of a large condenser. The dosage is usually 5-10 p.p.m., and is maintained for 5 min or a little longer. Within about 10 sec the water containing the chlorine has passed through the condenser and the greater part of the chlorine has attacked and has been absorbed by the incipient slime growth on the condenser tubes. Within a few seconds more, the water from this one condenser is mixed with water from other condensers to which no chlorine has been added and it is diluted and gradually absorbed by impurities in the water so that the residual chlorine comes down to a low level within a short time after having been added.

With sea water where chlorine is added to control mussel fouling a smaller dose is used, usually 2-3 p.p.m., but this is applied to all the water at the inlet to the station and may be applied continuously for several hours at a time. It is gradually absorbed by material in the water, and, in particular, by incipient slime growth on the condenser tubes and on other surfaces. Tests have shown that any residual chlorine is rapidly diluted and dispersed once the water has been returned to the sea; no figure higher than 0·2 p.p.m. being measurable off the outfall at Brighton for example. The time of passage through a station using sea water, however, is usually longer and may be of the order of 10-22 min, dependent upon the lengths of the intake and outfall culverts. Chlorine residuals found in outfall water during this investigation are recorded in Tables 2 and 3.

FAUNISTIC OBSERVATIONS

In the material collected in the intake and in the outfall waters of the power stations listed in Table 1, some representatives of nine freshwater and ten marine animal groups were found; the sixty-two marine and thirty-five freshwater species are listed in Tables 4 and 5.

The specific identification of the specimens collected was in some cases impossible owing to the larval and juvenile stages of the organisms. The faunistic composition of the intake and the outfall water is the same. Tables 4 and 5 show the specific composition of the zooplankton, and some benthic forms which were found. All the organisms listed were found alive. Besides qualitative data, some quantitative figures were obtained for Wakefield 'B' power station, and are given in Table 6. Protozoa were fairly numerous in all samples examined. No attempt at identification has been made, as this requires special methods and represents a separate problem. It was noticed, however, that some colonial Vorticellids (*Zoothamnium* sp.) occur in masses in the outfall of Roosecote power station.

Turbellaria. *Dalyellia* sp. was found in fairly large numbers in Leicester cooling pond.

Free-living Nematoda are represented in the collected material by five species found in fresh water and eight species found in sea water.

Three species of Hydrozoa have been recorded. Some observations on Coelenterata show that the larger medusae are damaged when pumped into the condensers.

Rotifera were very abundant in the material examined. As they need to be

examined alive only some of the Loricata were identified. None of the specimens examined showed any detrimental effects after being warmed up, chlorinated and circulated through the condensers. Five species of Rotifera in fresh water and one in sea water were identified. *Synchaeta littoralis*, found in the discharge of Roosecote power station, occurs in masses there at some times of year, and forms the bulk of the plankton in March.

Oligochaeta were very abundant in the cooling pond of Leicester power station, and in the outfall of Wakefield 'B' power station.

Table 4. *Species found in the intake and outfall of stations using sea water*

Species	Brighton 'B'	Carmarthen Bay	East Yelland	Plymouth	Poole	Roosecote
PROTOZOA	+	+	+	+	+	+
COELENTERATA						
HYDROZOA						
Cordylophora caspia (Pallas)						+
Leuckartia octona (Flemming)				+		
Obelia dichotoma L. (medusa)			+			
NEMATODA						
Anticoma limalis Bastian				+		+
Oncholaimus sp. (juv.)						+
Metachromadora sp.		+				
Chromadorita leuckarti (de Man)						+
Neochromadora poecilosomoides (Filipjev)				+		
Axonolaimus sp.				+		
Theristus sp.						+
Sphaerolaimus sp.				+		
ROTIFERA						
Synchaeta littoralis Rousselet						+
ANNELIDA						
OLIGOCHAETA						
Nais variabilis Piguet						+
POLYCHAETA						
Eulalia sp.			+			
Nereis diversicolor Müller						+
Polydora (larvae)					+	
Pomatoceros triqueter L.			+			
CRUSTACEA						
OSTRACODA						
Loxoconcha tamarindus (T. R. Jones)				+		
CLADOCERA						
Podon polyphemoides Leuckart						+
COPEPODA						
CALANOIDA						
Calanus finmarchicus (Gunnerus)	+	+	+	+	+	+
Paracalanus parvus (Claus)				+		
Pseudocalanus elongatus Boeck			+			
Temora longicornis (O. F. Müller)			+			
Eurytemora hirundoides Nordquist			+			
Centropages hamatus Lilljeborg			+			
Parapontella brevicornis Lubbock					+	
Acartia bifilosa Giesbrecht					+	
A. clausi Giesbrecht					+	
Paracartia grani (Sars)	+					
CYCLOPOIDA						
Oithona nana Giesbrecht			+			
Corycaeus anglicus Lubbock			+	+		

Species	Brighton 'B'	Carmarthen Bay	East Yelland	Plymouth	Poole	Roosecote
HARPACTICOIDA						
Canuella perplexa Scott			+			
Ectinosoma sp. (juv.)			+			
Euterpina acutifrons (Dana)			+	+	+	
Microarthridion littorale (Poppe)						+
Harpacticus littoralis Sars			+			
Tisbe furcata (Baird)			+	+	+	
T. gracilis (T. Scott)				+		
Sacodiscus fasciatus (Nordman)			+			
Alteutha interrupta (Goodsir)				+		
Amphiascopsis cinctus Claus	+		+			
CIRRIPEDIA (larvae)						
Nauplius	+				+	
Cypris	+		+	+		
ISOPODA						
Sphaeroma hookeri Leach						+
Sphaeroma serratum (Fabricius) (?) (juv.)			+			
Eurydice sp. (juv.)			+			
Gnathiidae (juv.)				+		
AMPHIPODA						
Corophium crassicorne Bruzelius			+			+
Gammarus locusta (L.)			+			+
Jassa falcata (Montagu)					+	
Caprella sp. (juv.)				+	+	
Gammaridea (juv.)			+			
MYSIDACEA						
Mesopodopsis slabberi (van Beneden)					+	
Praunus flexuosus (Müller)			+			
DECAPODA						
Portunus (?) sp. (megalopa)				+		
Palaemonetes varians (Leach)						+
Caridean larva				+		
INSECTA						
DIPTERA						
Orthocladiinae (larvae)						+
MOLLUSCA						
Gastropoda (larvae)					+	
Pelecypoda (larvae)			+			
Cardium sp. (juv.)				+		
CHAETOGNATHA						
Sagitta setosa J. Müller			+	+		
TUNICATA						
Coina sp. (larvae)	+					
Oikopleura dioica Fol.		+				

Four species of Polychaeta were identified in the collected material. The larval stages of *Polydora* were extremely abundant in the discharge from Poole Power Station, and *Nereis diversicolor*, larval and adult forms, at Roosecote.

Crustacea form the bulk of the material examined from larval and juvenile to adult stages. Seventeen species of Crustacea were recorded from fresh water and thirty-nine species in sea cooling water. In the cooling ponds of Leicester power station nine species of Cladocera, three species of Ostracoda and two species of Copepoda were found. Considering the relatively limited size of cooling ponds, the number of species shows that the environment has no detrimental effect. It should be emphasized that some of the Ostracods (*Cypridopsis vidua*) occur in

Table 5. *Species found in the intake and outfall of stations using fresh water*

Species	Carlisle	Ironbridge	Leicester	Wakefield 'B'	Worcester
PROTOZOA	+	+	+	+	+
TURBELLARIA					
Dalyellia sp.			+		
NEMATODA					
Trilobus pellucidus Bastian				+	
Dorylaimus sp. (juv.)			+		
Rhabditis (?) *terricola* Duj. (juv.)				+	
Butlerius (?) *butleri* Goodey				+	
Macrolaimus sp.				+	
ROTATORIA					
Brachionus quadridentatus Hermann		+			
B. urceolaris var. *sericus* Rousselet				+	
Euchlanis dilatata Ehrb.		+			
E. deflexa (Gosse)	+				
Keratella cochlearis (Gosse)	+			+	
ANNELIDA					
OLIGOCHAETA					
Tubifex sp.	+		+	+	
CRUSTACEA					
CLADOCERA					
Daphnia longispina O. F. Müller (juv.)				+	
Simocephalus sp. (juv.)			+		
Bosmina coregoni var. *lilljeborgi* (Sars)			+		
Ilyocryptus sp.			+		
Alona rectangula Sars		+	+		+
Rhynchotalona rostrata (Koch)		+	+		
Pleuroxus trigonellus (O. F. Müller)			+		
P. uncinatus Baird		+			
Chydorus sphaericus (O. F. Müller)		+	+		
OSTRACODA					
Heterocypris incongruens (Ramdohr)			+		
Cypridopsis vidua O. F. Müller			+		
Lymnocythere sp.		+	+		
COPEPODA					
Cyclops bicuspidatus Claus			+		
Eucyclops agilis (Koch)			+	+	
Microcyclops sp. (juv.)					+
Cyclops (nauplii)		+			
Calanoid nauplii	+				
HARPACTICOIDA					
Nitocra hibernica (Brady)		+			
INSECTA					
DIPTERA					
Orthocladiinae (larvae)	+	+	+	+	
CHIRONOMINAE					
Tanytarsus sp.		+			
Tendipes thummi Kieffer				+	
Simulium sp.	+				
ARACHNIDA					
HYDRACARINA					
Limnesia undulata (Müller)			+		
MOLLUSCA					
GASTROPODA					
Limnaeidae (juv.)			+		

masses in the above-mentioned ponds. Besides adult stages found in Leicester cooling ponds, such as females bearing eggs, naupli and juvenile forms of copepods were also found. This indicates that these Crustacea are able to reproduce in the cooling ponds. Table 4 gives details of the marine species collected, including larval and juvenile forms as well as adult stages. It seems that some of the Decapods (*Palaemonetes varians*) have a predilection for the warm water of the outfall, as they are very abundant in this particular place. In the spawning season females with eggs were very numerous, and later juvenile stages were also abundant.

Larval insects were found in both fresh and brackish water at Roosecote power station. They are chiefly larvae of Diptera (Orthocladiinae and Chironomidae—

Table 6. *Numbers of animals found in 50 l. samples at Wakefield 'B' power station, 25 September 1956*

	Sample number					Total in 250 l.
	1	2	3	4	5	
INTAKE WATER: 17·5° C						
Nematoda	51	91	82	60	143	427
Rotifera	18	27	45	11	179	280
Oligochaeta	10	10	5	2	25	52
Cladocera	5	–	–	–	–	5
Ostracoda	–	–	–	–	–	–
Copepoda	26	37	25	8	38	134
Arachnida	–	–	1	1	9	11
Diptera	12	16	14	12	20	74
Total	122	188	172	94	414	983
OUTFALL WATER: 24·4° C; Cl residual 0·2 p.p.m.						
Nematoda	115	55	150	169	139	628
Rotifera	291	61	88	168	219	827
Oligochaeta	60	40	51	8	11	170
Cladocera	–	1	6	2	2	11
Ostracoda	–	–	–	–	2	2
Copepoda	80	14	46	42	58	240
Arachnida	4	2	6	–	2	14
Diptera	100	182	140	55	43	520
Total	650	355	490	444	476	2412

the latter represented by three species). These larvae were very abundant in the Leicester cooling ponds.

Hydracarina (*Limnesia undulata*) occur in masses in cooling ponds at Leicester power station.

Mollusca have also been recorded in the cooling water. In fresh water, juvenile stages of Limnaeids were found, and in sea water larval gastropods and pelecypods were abundant in some of the samples. Specific identification, however, was not possible, because of their juvenile stages.

Chaetognatha were found in the cooling water of East Yelland and Plymouth power stations, and Tunicata at Brighton 'B' and Carmarthen Bay power station discharges.

The quantitative figures for fresh water, given in Table 6, show that at Wakefield 'B' power station the Nematoda and Rotatoria are predominant in the cooling water. The nematode fauna would lead one to assume that the river water

there is polluted. The second most numerous group in the material from Wakefield 'B' is Copepoda. In some 50 l. samples a fairly high proportion of Diptera larvae is noticeable.

In the intake samples the number of organisms varies from 94 to 414, and in the outfall water from 355 to 476 individuals. More individuals per litre were apparently found in the outfall than in the intake water. This is, however, not a statistically significant difference, because of the variation between the 50 l. samples and because all the 250 l. were sampled from the inlet before moving the equipment to the outfall, so that there may have been a real change in the incoming water. At least it is clear that there is no decrease in the number of planktonic organisms after being circulated through the plant. In this case, all organisms were also found alive.

Although zooplankton was the main subject of this paper, Tables 4 and 5 list the benthic forms found. They had been pumped into the plant with the cooling water and collected in the plankton net. Here also no detrimental effect was noticed, as these were also found alive. Some mechanical damage was, however, observed in the material collected, especially among the larger shrimps, but the percentage of the animals mechanically damaged was negligible.

DISCUSSION

It seems that the cooling water used by the power station situated by the sea or using fresh water from the rivers has no harmful effect on the species quoted in this report, since the organisms mentioned above, which had been exposed to a rise of temperature, chlorination, turbulence and other effects were found not only alive but also able to reproduce. It is difficult to say, however, whether the marine forms retain their normal vitality after being so treated, as no experimental work has been done. Some samples containing zooplankton (Crustacea) taken from the intake and outfall water from the sea, and left overnight at room temperature, show the same mortality rate. Observations on freshwater species indicate that they do not lose their vital capacity, and they can live and reproduce in cooling ponds, though the environmental conditions there are strongly disturbed. The mass occurrence of various species in cooling ponds confirm this supposition.

After circulation through the plant the organisms return to their natural environment very smoothly. This can be illustrated from observations at the shallow water reservoir at Roosecote power station, where temperature measurements were made by skin divers. In this particular place the warm water begins to rise about 4 m from the outfall and runs over the cold water layer. The thickness of this cold water layer is about 60 cm 5 m from the outfall, and it gradually increases as the warm water spreads out over the surface until equilibrium is reached. The organisms which are discharged with the warm water fall gradually into the cold water layer which is their natural environment. It will also be noted that benthic fauna will only be affected by warm water in the immediate vicinity of the outfall.

A similar explanation can be given for the effect of chlorination of the water.

After being injected the chlorine content of the water drops rapidly to a negligible harmless amount. It may be asked why chlorine is used to control mussels and other organisms when it has no apparent effect on zooplankton. Chlorine has a harmful effect on non-planktonic organisms which are sedentary in habit when they are exposed to relatively high concentrations for long continuous periods of time.

The oxygen concentration of the water discharged from the cooling water system is either the same as in the natural environment or even higher owing to powerful turbulence. Thus, this important factor in aquatic life is not disturbed. This does not necessarily mean that all species of freshwater and marine organisms exposed to these conditions will survive.

In this report, which is intended to give only a general picture of the effect of power station activity on the organisms found in the cooling water, only a small number of species were examined, owing to the limited number of samples taken. If a full and comprehensive survey is to be made, systematic annual observations over a long period will have to be carried out.

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SUMMARY

1. A number of power stations were surveyed to see whether the cooling water system had any effect on the aquatic invertebrates found in fresh and sea water.

2. The samples of zooplankton were collected in the intake and in the outfall waters for quantitative and qualitative investigations.

3. Some thirty-five freshwater and sixty-two marine species were identified.

4. No detrimental effect on the organisms found was observed. They were alive after being circulated through the condensers.

5. No difference in fauna composition between the intake and the outfall was found from the qualitative and quantitative points of view.

6. Freshwater forms are able to live and reproduce in the cooling ponds of the power station.

7. The chemical and physical features of the cooling water was given.

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AN EXPERIMENTAL STUDY OF THE SEARCHING BEHAVIOUR OF THE PREDATORY COCCINELLID BEETLE *ADALIA DECEMPUNCTATA* (L.)

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(With 7 Figures in the Text)

The searching behaviour of insect predators has received little attention, with two notable exceptions. Fleschner (1950) compared the searching capacity of the last instar larvae of three predators of the citrus red mite, *Paratetranychus citri* (McGregor), one of the predators being the coccinellid beetle *Stethorus picipes* Casey. Banks (1954, 1957) studied the behaviour of first-instar larvae of *Propylea quatuordecimpunctata* (L.), and of the first and fourth-instar larvae of *Adalia bipunctata* (L.) and *Coccinella septempunctata* L.

The aim of the present laboratory study of the predatory coccinellid beetle *Adalia decempunctata* (L.) has been to investigate the mortality which occurs before dispersal from the egg batches, to estimate the effect of topography and feeding on the searching behaviour of the larvae, and to examine the searching capacity of individuals of different instars and their survival, and finally, the effect of prey population density on the rate of increase of the coccinellid.

The coccinellid beetle *A. decempunctata* (L.) and the nettle aphid *Microlophium evansi* (Theob.), which was used for feeding the beetles, were reared as described previously by Dixon (1958). Until they hatched, egg batches of *Adalia decempunctata* were each isolated in celluloid pill boxes provided with moist filter paper to maintain a relatively high humidity. These, and the vials in which larvae and adults were reared, were kept in an incubator maintained at 21° C and 66% R.H. during the day. Fluorescent lighting mounted above a window in the roof of the incubator gave a light intensity of 1398 metre-candles for 16 h a day at shelf level where eggs, larvae and adults were placed. This photoperiod was chosen as it gave best results in rearing the nettle aphid. As few animals thrive well in constant conditions both heating and lighting were turned off at night.

PREDISPERSAL BEHAVIOUR IN *ADALIA DECEMPUNCTATA*

Where a predatory insect lays its eggs in batches it is expected that if cannibalism occurs, it must either have some adaptive significance or occur to a limited extent only. The first part of the paper considers the effect of cannibalism on predispersal mortality in *Adalia decempunctata*, a batch-laying species.

In the field, egg batches of *A. decempunctata* contain from three to thirty eggs (average, fourteen) and larvae may hatch successively over a period of several hours. For about an hour, while the cuticle hardens and darkens, a newly emerged

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coccinellid larva remains on top of its egg shell, and during this period it is apparently incapable of defending itself from any older larvae in the same batch. Several authors have found that in a number of species of coccinellid cannibalism occurs before the larvae disperse from the egg shells, but it is not clear whether cannibalism here meant the consumption of eggs alone, or of both eggs and newly emerged larvae. In order to obtain an estimate of the frequency of cannibalism in *A. decempunctata*, batches of eggs were isolated in celluloid pill boxes, and examined 48 h after hatching was complete. Of the 8029 eggs in these 766 batches, 1470 eggs were devoured, but only seven of the larvae which emerged were eaten; six of these larvae had only partly emerged, and one had completely emerged. Hence cannibalism appears to be almost restricted to egg eating.

The interval before dispersal from the eggs varies from 12 to 24 h for *A. decempunctata*. However, batches in which the larvae hatch at approximately the same time may be classified for experimental purposes into three groups according to the general appearance and activity of the larvae: first 'freshly emerged', when the larvae have just hatched and are still pale in colour; second 'active', when the larvae have darkened and begun to move and to palpate neighbouring larvae, but still adhere to the egg shell by means of the anal disc at the tip of the abdomen; and third 'predispersal', when the larvae leave the vicinity of their own egg shell and move actively over and around all the egg shells. Batches from each of these categories were selected and two freshly emerged larvae from another batch were placed on each to determine whether they would be eaten. The batches were examined again 24 h later.

Larvae placed on batches of freshly emerged and active larvae were not eaten, but of ten placed on five batches of predispersal larvae, six were eaten. That is, although freshly emerged larvae are apparently unable to defend themselves, since their cuticle is still soft and they are unable to walk, they are attacked only by predispersal larvae ($P < 0{\cdot}01$), although predispersal larvae do not eat one another.

In another experiment batches of freshly emerged larvae were selected, and these were presented with freshly emerged larvae and recently laid eggs both of which had been killed by keeping them at a temperature of -7° C for 12 h. The same procedure was then followed using batches of larvae presented with dead larvae and eggs as before, but this time the eggs contained well-developed embryos which are recognizable by their dark colour. All the eggs were eaten, but none of the larvae. Therefore, irrespective of the stage of development of a dead embryo within an egg, on reaching the active phase already described larvae will suck out the egg contents, although on the other hand they will not attack dead freshly emerged larvae. If, however, dead larvae are left on the batch until the living larvae reach the predispersal phase, then they are usually attacked and eaten, so that dead larvae are in fact acceptable as food.

As eggs which have not hatched are likely to be eaten by larvae which emerge earlier in a batch, it is informative to have an estimate of the viability of these remaining eggs. Therefore, batches were chosen in which all the larvae were active, and some unhatched eggs containing well-developed embryos still remained

undamaged. The larvae were removed and 48 h later the eggs were examined again. Of the thirty-one eggs only five hatched successfully, although in thirteen of them the chorion had split and in five the head of the larva was protruding. Therefore, most of the eggs which are eaten, even though they may contain well-developed embryos, would not normally hatch successfully. The consumption of eggs by active larvae, and of dead larvae by predispersal larvae is therefore an adaptive behaviour pattern since if the larvae obtain food before dispersal they are able to survive longer and so stand a greater chance of finding prey. That freshly emerged larvae are not eaten by active larvae is also advantageous since it allows for variation in the time of hatching of eggs in the same batch.

INFLUENCE OF TOPOGRAPHY ON THE MOVEMENT OF LARVAE

Irrespective of the position of a light source, poorly fed larvae move upwards when placed on a vertical surface. Larvae are positively phototactic, however, when placed on a horizontal surface. Their movement on a vertical surface may therefore be a result of negative geotaxis and positive phototaxis, in which the former is dominant. This type of behaviour allows the coccinellid larvae to reach the apex of a plant stem, which is the region of the plant preferred by their prey.

The effect of leaf topography on the movement of poorly fed third-instar larvae was determined by observing their behaviour on a triangular hastate leaf, 32·5 cm long, of *Typhonium giraldii* (Baroni) Engl. (Araceae). Larvae were released on the petiole of the leaf and their position on reaching the lamina, whether on the area between veins, on prominent veins or the rim, was noted every 10 sec. The rim was taken to be a track running parallel to the edge of the leaf, extending the width of one third-instar larva from the lamina edge towards the midrib. Observations were made of larvae on the lower surface only, as preliminary experiments showed that larvae spent much less time on the upper surface of the leaf than on the lower.

If the larvae move at random on a leaf, the number of times larvae would be expected on different areas of the leaf can be calculated by weighing the corresponding parts of a paper replica of the leaf. However, it was found that larvae do not move at random over the lower surface of a leaf ($P < 0{\cdot}01$), but tend to follow the surface irregularities such as the veins or rim, and since nettle aphids are found mostly on the veins or very close to the edge of the leaves (Table 1), this behaviour increases a larva's chance of finding aphid prey.

THOROUGHNESS WITH WHICH LARVAE SEARCH AN AREA

Many predators and parasites are known to pursue a more tortuous path after parasitizing or feeding upon their respective hosts or prey. Where the host individuals or prey are aggregated together, it is advantageous to a parasite or predator to search the area more thoroughly where it has already encountered host or prey individuals, as by doing so its chance of finding more is increased. The duration of this more thorough search after feeding may be very short (Banks 1957).

Two vertical wooden cylinders 3·2 mm in diameter were marked off at 2·5 cm intervals. Cylinders of this diameter were used, as first-instar larvae often could not keep hold of cylinders of any greater diameter. A cylinder 45·7 cm long was used for first- and second-instar larvae and one 78·7 cm long, for third- and fourth-instar larvae. A 100 W bulb was suspended above the cylinders and gave a light intensity of 129 metre-candles at the base, and 430 and 6450 metre-candles, respectively, at the apices of the cylinders.

The effect of different feeding rates upon the movements of *Adalia decempunctata* larvae was then observed. First- and second-instar larvae were fed with first-instar aphids. Third- and fourth-instar larvae were given third-instar aphids. The average number of aphids each larva consumed each day was calculated. The larvae were placed at the bottom of the cylinders, and then their position each time they changed vertical direction, and also their final position, were recorded. Observations were made daily for a period of 5 min, or until the larva reached the

Table 1. *The number of times ten third-instar* Adalia decempunctata *larvae were observed on different parts of a leaf of* Typhonium giraldii, *and the distribution of 600 individuals of* Microlophium evansi *on* Urtica dioica *leaves*

	Part of leaf		
	Area between veins	Veins	Rim
Percentage of total leaf area	88·5	8·4	3·1
Number of times larvae observed	149	288	395
Distribution of aphids (%)	11·5	54	34·5

apex of the cylinder or returned to the base. The sum of all the records for an individual gives an index of its rate of change of vertical direction at a particular feeding rate. Second-, third- and fourth-instar larvae made an additional $2{\cdot}6 \pm 0{\cdot}8$, $4{\cdot}3 \pm 0{\cdot}7$, and $2{\cdot}4 \pm 0{\cdot}6$ turns, respectively, for an increase in consumption of one aphid each day (multiple regression analysis). Starved first-instar larvae made an average of 3·1 turns in an average distance of 78·0 cm. Starved second-, third- and fourth-instar larvae made an average of only 0·4 turns in an average distance of 164·9 cm, and this difference in behaviour is strongly significant ($P < 0{\cdot}01$).

Different feeding rates in the laboratory simulate conditions of different population densities of prey in the field. At high aphid population densities therefore, larvae will turn frequently and so tend to confine their search to a small area. At low aphid population densities turning is rarer, and so their chance of arriving at more distant aphid colonies is increased. This behaviour keeps the larvae close to any aphid colonies which they may find, and subsequently when these are exploited enables them to find fresh colonies. Hence, in addition to the change in behaviour which occurs immediately after feeding, in *A. decempunctata* there is also a more persistent effect which is especially adaptive where the prey is diffusely aggregated, a condition found in many species of aphid on which this coccinellid

feeds. As starved first-instar larvae cross their own tracks more often than do starved larvae of the succeeding instars, they have a greater tendency to confine their search to a small area and therefore stand more chance of finding a colony by which the adult has laid eggs if the species of aphid is gregarious, but less chance of finding individual aphids if the individuals of the species of aphid are diffusely distributed.

To test the ability of older starving larvae to abandon the apex of a stem which their responses to gravity and light would normally lead them to occupy, recently moulted fourth-instar larvae, fed a few aphids only, were placed at the base of the

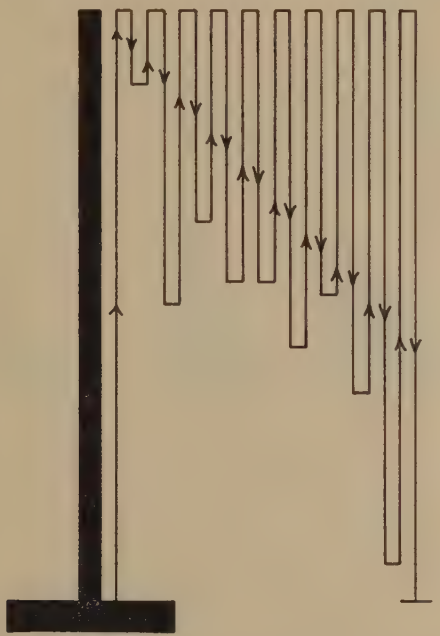

Fig. 1. The track of a recently moulted fourth-instar *Adalia decempunctata* larva on a vertical cylinder.

45·7 cm cylinder already described. The number of times a larva changed its vertical direction was recorded until it left the cylinder. After the first day larvae were kept without food and then tested every 24 h until they died.

On the first day larvae tend to follow a pattern of movement similar to that shown in Fig. 1. They climb to the apex of the cylinder and begin to descend, but then turn upwards again a short distance from the apex. This manœuvre may be repeated several times, but there is a marked tendency to descend further down the cylinder on each successive occasion until finally they reach the base of the cylinder. The tendency to revisit the apex of a cylinder where there are no aphids decreases as the period of starvation increases (Fig. 2; $P<0{\cdot}01$). Although the

experimental situation here is very much simplified when compared with a plant stem, observations suggest that the results also apply to these more complicated situations. In the field this type of behaviour serves to prevent the larvae from becoming trapped at the apices of plant stems, and also allows them to leave these areas more quickly when starved.

Larvae which were placed on a similar, horizontal cylinder returned to the

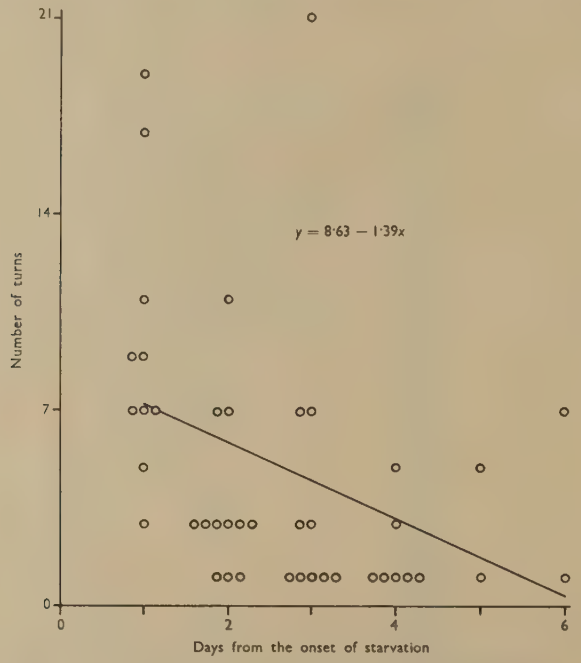

Fig. 2. The number of turns executed on a vertical cylinder in relation to the number of days from the onset of starvation for fourth-instar *Adalia decempunctata* larvae.

base of the cylinder each time. Therefore it seems that the response to gravity is influenced by the degree of starvation of the animal.

EFFICIENCY IN CAPTURING PREY

Larvae of *Adalia decempunctata* seem to respond to an aphid only after touching it with the head or fore limbs. Adults appear to require actual palpal contact with their prey before showing a response.

Corked vials were filled with water and the petiole of a freshly cut nettle leaf was inserted through a hole in each cork. Then individuals of a selected instar of *Microlophium evansi* were placed on each leaf and left to insert their stylets. Individuals of *Adalia decempunctata* which had recently hatched or moulted and

were moving about actively, were set to capture these aphids, and the number which avoided the coccinellids was noted. Records were restricted to situations where aphids were feeding in the direct path of the coccinellid. Such a situation is defined as an *encounter*. A maximum of twenty encounters was allowed for each coccinellid, but if it captured an aphid in less than twenty, no further records were taken after the capture had been made.

Recently emerged larvae of *A. decempunctata* are able to capture an average of only one first-instar aphid out of every five they encounter, but there is a definite increase in efficiency in capturing aphids as the larvae become older. The efficiency of the adult, however, lies only between that of a second- and a third-instar

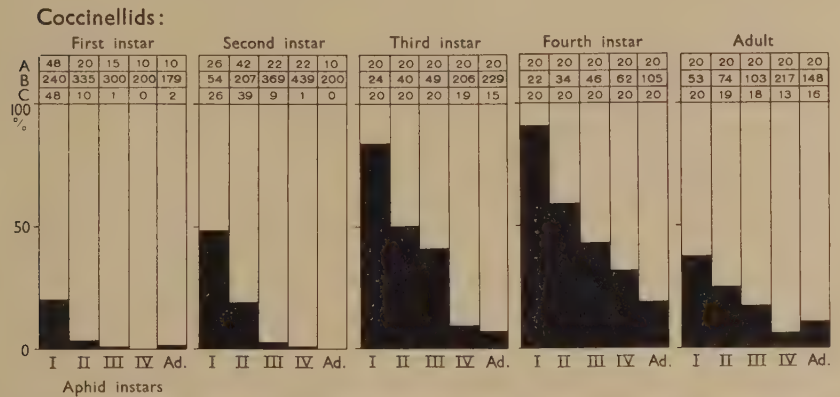

Fig. 3. The efficiency (percentage of encounters resulting in capture) of *Adalia decempunctata* in capturing *Microlophium evansi*. A, number of coccinellids tested; B, encounters observed; C, aphids captured.

larva (Fig. 3). The shininess, coloration, and the hemispherical shape which would make the adult appear large viewed from any angle, probably make it far more conspicuous than the larvae, which are dull, black and flattened in form. Hence aphids have more warning when an adult approaches, and tend to avoid capture effectively by walking away or dropping off the plant (Dixon 1958).

THE TIME TAKEN TO CONSUME PREY

As the amount of time available for searching must vary with the instar of coccinellid, being relatively short in the first instar, it is of interest to know how long larvae of each instar take to consume their prey, and hence the maximum amount of time they can spend searching. Individual coccinellids were allowed to capture an aphid and the time taken to eat the aphid was noted (Table 2). Larvae tend to take longer to consume aphids of each successive instar, but a first-instar larva takes as much as thirty times as long as a fourth-instar larva to consume a first-instar aphid. The actual proportion of time spent feeding and its effect on the survival of larvae is considered later.

THE EFFECTS OF APHID POPULATION DENSITY

(*a*) *On the ability of larvae to capture their first prey*

If unfed first-instar larvae are provided with one or more first-instar aphids on a small nettle leaf, there is enough larval food present to maintain life for a short period. When fifty larvae were each provided with one first-instar aphid, only twenty-eight captured an aphid, while out of sixty-five each provided with three first-instar aphids, altogether sixty-one captured an aphid. Of the twenty-eight out of fifty unfed larvae which captured an aphid when provided with one aphid each day, twenty-three then survived to make a second capture.

Table 2. *The average time taken by* Adalia decempunctata *larvae to consume* Microlophium evansi

	Coccinellid instar							
	First		Second		Third		Fourth	
Aphid instar	Number	Average time taken (min)	Number	Average time taken (min)	Number	Average time taken (min)	Number	Average time taken (min)
First	47	118·5 ± 11·38	24	38·33 ± 5·65	20	14·25 ± 1·17	20	4·3 ± 0·38
Second	7	256·4 ± 41·63	30	84·97 ± 8·54	20	26·5 ± 2·82	20	10·15 ± 0·86
Third	1	920 (not finished)	8	181·88 ± 24·51	20	56·0 ± 5·77	19	32·63 ± 4·44
Fourth	–	–	1	215·0	16	136·4 ± 15·41	17	54·7 ± 5·64
Adult	–	–	–	–	15	96·66 ± 9·9	20	62·1 ± 10·96

To determine the efficiency of first-instar larvae of different ages in capturing their prey, thirty larvae were each placed on a nettle leaf on which a number of first-instar aphids were feeding, and the number of encounters which a larva made before it captured an aphid were recorded. The larvae were tested every 24 h so that they captured and consumed an aphid each time. The experiment was discontinued after the fourth day in order to avoid any abnormal effects arising as a result of premoulting behaviour.

The efficiency of first-instar larvae in capturing first-instar aphids increases from one capture in an average of 4·8 encounters on the first day to one in 1·5 encounters on the fourth day (regression analysis $P < 0{\cdot}01$). Therefore the likelihood of a first-instar larva capturing its first aphid depends mainly upon the prey population density, but having once captured an aphid a larva is more likely to capture prey which is present. This is partly due to an increase in efficiency in capturing prey.

(*b*) *On the survival of larvae in each instar*

In order to compare the nutritive requirements of each instar of coccinellid, previously unfed first-instar larvae were provided with different numbers of aphids, and every 24 h consumed aphids were replaced. From these observations (Table 3), the feeding rate at which 50% of the larvae survived, and also the time spent in this instar were calculated. Then once the number of aphids which had

to be provided each day for 50% survival in the first instar had been determined approximately, more larvae were fed at this rate, and those reaching the second instar were again provided with different numbers of aphids. Hence, the approximate number of aphids for survival of 50% of the larvae in this instar was found, and so on. The number of aphids provided each day for survival of 50% of the larvae in the different instars was $0{\cdot}95 \pm 0{\cdot}14$ first-instar aphids, $2{\cdot}66 \pm 0{\cdot}22$ first-instar aphids, $1{\cdot}07 \pm 0{\cdot}11$ third-instar aphids, and $1{\cdot}93 \pm 0{\cdot}15$ third-instar

Table 3. *The effect of the number of aphids provided each day upon percentage survival in, and duration of, each instar in* Adalia decempunctata

Number of aphids provided each day	Number of larvae tested	Number of larvae surviving	Survival (%)	Total number of aphids eaten	Average duration of instar (days)
FIRST-INSTAR LARVAE					
1	28	15	54	4·47 ±0·38	5·67 ±0·48
2	13	12	92	6·08 ±0·36	4·25 ±0·22
3 (First-instar aphids)	60	56	93	7·16 ±0·23	3·68 ±0·13
6	42	39	93	8·51 ±0·40	3·03 ±0·06
8	113	105	93	10·75 ±0·31	3·05 ±0·04
SECOND-INSTAR LARVAE					
1	21	0	0	–	–
2	17	2	12	10·5 ±1·5	6·0 ±1·0
3 (First-instar aphids)	15	13	87	10·92 ±0·87	4·08 ±0·26
4	23	17	74	16·29 ±1·29	4·47 ±0·32
5	18	17	94	13·59 ±0·58	3·24 ±0·14
THIRD-INSTAR LARVAE					
0·5	13	0	0	–	–
1 (Third-instar aphids)	20	11	55	7·36 ±0·56	8·0 ±0·63
2	15	14	93	7·64 ±0·48	4·36 ±0·20
FOURTH-INSTAR LARVAE					
1	10	0	0	–	–
2	10	6	60	15·50 ±0·67	9·50 ±0·56
3 (Third-instar aphids)	10	9	90	17·0 ±1·05	8·33 ±0·44
4	10	8	80	23·25 ±1·13	7·13 ±0·40
10	10	9	90	39·33 ±1·18	5·44 ±0·18

aphids for the first-, second-, third- and fourth-instar coccinellid larvae respectively (probit analysis).

As six first-instar aphids are equivalent in mass to one third-instar aphid (Table 6), each successive instar of *Adalia decempunctata* requires a higher feeding rate for 50% survival. The duration of each successive instar is longer than the one which precedes it.

(c) *On the rate of larval development and survival, and on adult size*

Adalia decempunctata adults taken in the field are relatively constant in size, but adults of various sizes can be reared in the laboratory, depending upon the amount of food provided to the larvae. It is possible, therefore, to estimate the number of aphids eaten by a coccinellid during its larval development in the field, and also the time it takes to reach the adult stage.

Previously unfed larvae were provided with different numbers of first-instar aphids (Table 4) as in the previous experiments. Every 24 h consumed aphids were replaced. When they reached the second instar, larvae were fed an equivalent number of third-instar aphids (Table 6). The higher the rate of feeding, the greater the rate of development and the proportion of larvae surviving to become adults, until there are signs of satiety when approximately fifteen third-instar aphids are provided each day (Table 4, Fig. 4). As the pupal stage lasts 5 days, irrespective of the number of aphids eaten by the larva, the minimum time required for development from eclosion to emergence of the adult is 15 days at about 21° C.

Adults from the pupae obtained in this experiment were allowed to harden after emergence, and then their breadth and length were measured. For each individual, the product of these measurements was used as an index of its size.

Table 4. *The effect of the number of third-instar aphids provided each day to each larva on the rate of development, survival, and adult size in* Adalia decempunctata

Number of aphids provided each day to each larvae	Number of larvae tested	Number of larvae surviving	Duration of development (days)
1	39	0	–
2	42	8	20·88 ±0·87
3	30	11	18·73 ±0·54
4	25	12	16·5 ±0·48
6	20	14	14·21 ±0·28
8	20	16	13·31 ±0·29
10	30	21	13·57 ±0·22
15	20	17	10·24 ±0·20
20	20	17	10·18 ±0·13

The adults were then killed, desiccated and weighed. Size and weight of adults are both greater when the larvae are provided with a large number of aphids each day (Fig. 5). If the size and weight of the adults are compared, it is found that at the higher feeding rates the adults are relatively heavier, possibly due to deposition of fat.

A number of pupae of *A. decempunctata* were taken in the field with various aphids. The forty-four adults which emerged from these pupae had an average size index of 11·99 ±0·30 and an average weight of 2·14 ±0·07 mg. Adults of the same average size and weight were reared in the laboratory from larvae provided with twenty aphids each day, and these ate an average total of 76·74 ±1·35 third-instar aphids. This implies that in the field coccinellid larvae eat an average quantity of aphids equivalent to approximately seventy-seven third-instar individuals of *Microlophium evansi*, and complete their development in about 15 days, if the temperature averages about 21° C during the day. Some very large adults were obtained from pupae taken in the field, and the largest of these had a size index of 16·63, and weighed 3·4 mg. The absence of very small adults in the

field may be due to selective mortality shortly after emergence from the pupa, but this is discussed more fully later (p. 276).

THE AREA OF DISCOVERY OF THE LARVAE

Nicholson (1933, p. 141) states that the area which an animal searches can be

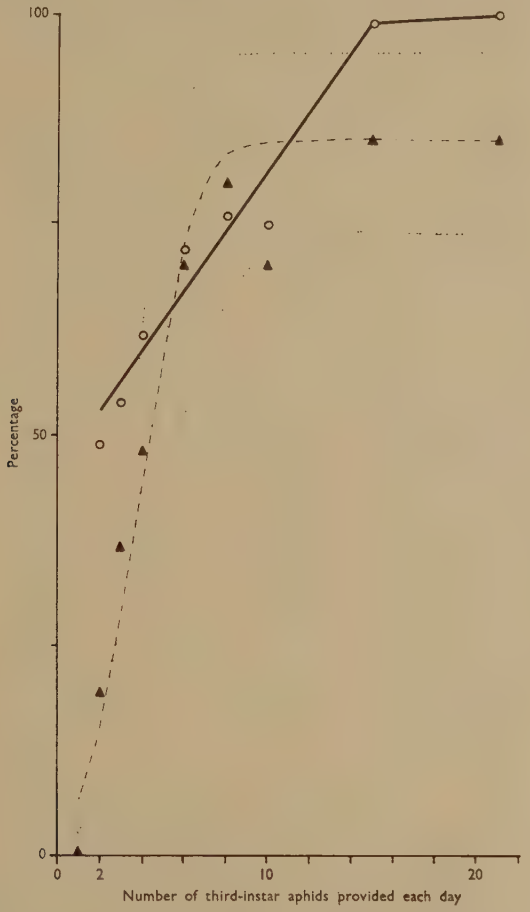

Fig. 4. The effect of the number of third-instar aphids provided each day to larvae on the average rate of development from eclosion to pupation, and the percentage of larvae surviving to become adults in *Adalia decempunctata*. (o——o, average rate of development; ▲ – – – ▲, mean percentage of larvae surviving; ....., 95% and lower fiducial limits of percentage survival.)

considered in this way: the total area searched by an animal is the 'area traversed', that is, the product of the total distance travelled and the range of perception. He assumes that this area is independent of the density of the objects sought by

the animal. While it would be tedious to follow an animal throughout its life in order to determine the distance it travelled in that time, an index of the distance which it travels is provided by the sum of the average speeds of locomotion of an individual on each successive day of its life. For *Adalia decempunctata* the average

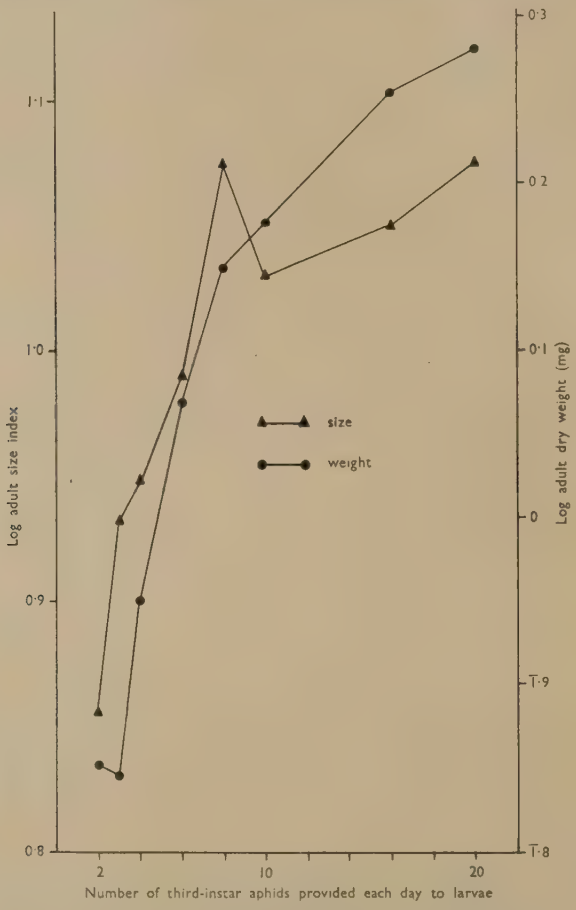

Fig. 5. The effect of the number of third-instar aphids provided each day to larvae on the average size and dry weight of *Adalia decempunctata* adults.

speed of the larvae was calculated from the distance which larvae travelled on a vertical cylinder, and the time taken to do so. The sum of the average speeds recorded each day for a single individual gives a figure which will be referred to as the 'distance index'. This takes into account both the speed of locomotion and the length of life of the larva, or duration of the instar, at a particular feeding rate. The results for each instar are summarized in Table 5. In each successive instar,

unfed larvae travel a greater distance before they succumb to starvation, and larvae which consume very few aphids each day live longer than larvae of the same instar which consume rather more. Since larvae apparently do not see their prey, and must touch the prey with the head or fore limbs to recognize it, a larva's range of perception is taken to be the distance between the furthest projecting hairs on the outer surface of the fore limbs, which remains constant within an instar (Table 7). Therefore, the area a larva traverses while in a particular instar is much greater if the larva is poorly fed, and as different feeding rates simulate

Table 5. *The effect of the average number of aphids consumed each day on the 'distance index' (see text) of* Adalia decempunctata *larvae*

Average number of aphids consumed each day		Number of coccinellid larvae tested	Average distance index
FIRST-INSTAR LARVAE			
0	first-instar	17	16·15 ± 2·36
0·75-1·0	first-instar	9	39·27 ± 5·26
1·0 -2·0	first-instar	9	23·95 ± 2·97
SECOND-INSTAR LARVAE			
0	first-instar	19	42·11 ± 5·33
1-2	first-instar	2	88·65 ± 37·77
2-3	first-instar	12	79·20 ± 10·95
3-5	first-instar	24	37·77 ± 3·25
5-8	first-instar	19	47·63 ± 4·17
THIRD-INSTAR LARVAE			
0	third-instar	25	63·96 ± 7·77
1-2	third-instar	19	219·91 ± 19·81
2-4	third-instar	21	70·03 ± 6·17
4-7	third-instar	19	64·49 ± 4·90
FOURTH-INSTAR LARVAE			
0	third-instar	13	120·65 ± 14·07
2- 3	third-instar	21	282·04 ± 21·31
4- 8	third-instar	12	142·42 ± 17·22
8-12	third-instar	7	125·20 ± 25·25
12-16	third-instar	11	114·94 ± 17·73

different population densities of its prey, the area traversed by *A. decempunctata* larvae will vary with the population density of their prey.

Nicholson (1933, pp. 144, 165) refers to the area effectively traversed as the 'area of discovery' of the species; if an average individual captured only half the number of prey which it met, its area of discovery would be half the area it traversed. He assumes that the efficiency of capture of an average individual is constant, and therefore its area of discovery is constant. In order to capture individuals of *Microlophium evansi*, *Adalia decempunctata* larvae must move almost continuously, even in relatively dense populations of the aphid, as the latter tends to avoid the larvae and to be diffusely distributed over the host plant. Use of the distance index as a measure of the distance travelled is therefore justifiable until satiation of the individual comes into effect. When a large number of aphids is eaten each day the distance index is possibly an overestimate, as the larvae were

tested under conditions in which they are more likely to walk. Therefore the distance travelled at the higher feeding rates is probably less than the distance index indicates. Therefore, assuming even that efficiency of capture is independent of prey population density, which is unlikely as poorly fed larvae are probably more efficient, in *A. decempunctata* the area of discovery decreases with increasing prey population density.

LARVAL POWERS OF SURVIVAL

In order to complete an instar in a certain time, *Adalia decempunctata* larvae must eat a certain number of aphids in that time, and their ability to do so depends

Table 6. Microlophium evansi—*the weights of different instars and the age distribution of a population being attacked in the field by* Adalia decempunctata *larvae*

Instar	Weight (mg/100 aphids)	Equivalent in aphid units	Population (Number)	Population (%)
First	2·05	0·16	429	39·6
Second	6·9	0·54	410	37·8
Third	12·7	1·0	118	10·9
Fourth	25·0	1·97	34	3·1
Adult	28·5	2·24	93	8·6

upon the efficiency of the larvae in capturing aphids, the abundance of aphids, the total area the larvae search and also upon the age distribution of the prey. A comparison of their dry weights gives an estimate of the number of aphids of each instar equivalent to a third-instar aphid (one 'aphid unit') (Table 6). Hence it is possible to estimate the number of aphid units captured by individuals of each

Table 7. *Estimated index of the population density of prey required for 50% survival in* Adalia decempunctata *larvae*

Coccinellid instar	Number of aphid units captured per 100 encounters (U)	Number of aphid units required for 50% survival (S)	Percentage of time spent searching	Mean range of perception of twenty individuals	Area index corrected for time spent feeding (A_e)	Prey population index $\left(\frac{S}{A_e U}\right)$	Prey population index ratio
First	2·14	0·72	94·78	0·94 ±0·03	34·98	0·00962	12·0
Second	7·17	1·75	95·04	1·28 ±0·04	96·35	0·00253	3·2
Third	21·76	7·36	96·14	1·67 ±0·05	353·07	0·00096	1·2
Fourth	28·14	15·50	97·22	2·5 ±0·04	685·50	0·00080	1·0

instar of coccinellid in a hundred encounters, when attacking an aphid population of the age distribution shown in the table. Likewise the number of aphids required for 50% survival in each coccinellid instar (p. 267) can be converted into aphid units (S in Table 7).

An index of the prey population density required for survival of 50% of the coccinellids in a particular instar is of value in comparing the relative ability of

larvae in each instar to survive. This can be obtained from the equation $P = S/A_c.U$, where P is the index of prey population density, S the number of aphid units required for 50% survival, A_c the area index corrected for time spent feeding, and U the total number of aphid units captured per 100 encounters. When this index is calculated for each instar it is found that first-instar larvae require an aphid population density twelve times greater than that required by fourth-instar larvae (Table 7). This difference would be even greater if the pronounced tendency of first-instar larvae to recross their tracks were taken into consideration. The increase in the index of the area which individuals of successive instars traverse is partly offset by the increase in the number of aphid units required for 50% survival.

A decrease in the proportion of young aphids would greatly increase the aphid population density required for survival in the first instar. If the aphid age distribution in Table 6 were reversed so that there was a predominance of older aphids, a condition which could occur in an older population or as a result of predation, the aphid population density required for survival of 50% of the first-instar larvae would be thirty times greater than that for fourth-instar larvae. Oviposition near or in young aphid colonies of very high density is therefore necessary for the survival of first-instar larvae, and the chance of death from starvation is greatly reduced in successive instars.

The values used for a larva's efficiency in capturing prey in the above calculations are based upon observations of newly hatched or newly moulted larvae, but as first-instar larvae increase in age their efficiency in capturing prey also increases. On the fourth day they are as efficient as newly emerged second-instar larvae in capturing first-instar aphids. Therefore even within the first instar the aphid population density required for 50% survival will decrease as the coccinellids become older. This may also be true for individuals in the later instars, although possibly not to such a marked extent. The consumption of eggs and dead or dying larvae by larvae before they disperse from the egg batch would also decrease the aphid population density required for survival of 50% of the individuals in the first instar.

ADULT ACTIVITY AND OVIPOSITION

Gilliat (1935) noticed that well-fed adults of the predatory coccinellid *Stethorus punctorum* Lec. tend to remain at rest on leaves for periods of from ½ to 1 h, and Putman (1955) observed that if food is scarce, activity is prolonged in *S. punctillum* Weise, and also fewer eggs are laid.

To investigate how the rate of feeding affects the activity of *Adalia decempunctata* adults and their rate of oviposition, forty females were each provided with a fixed number (4, 8, 16 or 24) of third-instar aphids. Every 24 h consumed aphids were replaced. The coccinellids were allowed 5 days to accommodate to these feeding conditions, and were then transferred to celluloid tubes 21·6 cm long and 1·5 cm in diameter and closed at each end by a rounded celluloid cap. These tubes were laid on a bench beneath fluorescent lighting which gave a light intensity of

376 metre-candles at that level, and a screen was placed between each of the tubes so that adults could not stimulate one another. The females were allowed to settle, and then every 10 min records were made of any individuals which were walking. Observations were made over a period of $2\frac{1}{2}$ h every 5 days until each adult had been tested four times. Individuals provided with four aphids per day were twice as active as those provided with twenty-four, and those provided with eight and sixteen were intermediate in their activity (regression analysis, $P < 0{\cdot}01$).

Before the above experiment commenced, each female was allowed to mate, and then to mate again 2 weeks later. All eggs were removed from the vials three times a day as adults will consume them when aphids are scarce. The number of eggs laid each day was counted after the first 5 days. There was no evidence to show that females ate any eggs during the experiment. After 20 days the adults were killed, their ovaries removed and stained in acetocarmine. The numbers of mature eggs, and of immature eggs at least three-quarters the size of mature eggs,

Table 8. *Effect of the number of third instar* Microlophium evansi *provided each day on the number of mature and almost mature eggs present in the ovaries of* Adalia decempunctata

Average number of third-instar aphids provided each day	Average number of mature and almost mature eggs present in the ovaries
4	3·00 ± 1·14
8	12·78 ± 2·31
16	18·25 ± 1·75
24	15·36 ± 2·44

were both noted (Table 8). The number of eggs laid and the number of mature and nearly mature eggs in the ovaries of *A. decempunctata* increase as the number of aphids eaten each day increases (Fig. 6).

OVIPOSITION SITES OF *ADALIA DECEMPUNCTATA* IN THE FIELD

In 1956 a number of egg batches of *Adalia decempunctata* were collected from an aphid-infested lime tree (*Tilia* × *vulgaris* Hayne) in the University Parks, Oxford. The species of aphid causing the infestation, *Eucallipterus tiliae* (L.), does not aggregate in dense colonies, but is diffusely distributed over its host, and of 319 leaves taken from the periphery of the tree, sixty-one were infested with aphids. The most abundant species of coccinellid adult attacking *E. tiliae* was *Adalia decempunctata*. However, a few individuals of other species were seen, and batches of very large eggs (*Coccinella septempunctata*) and orange eggs (*Adalia bipunctata*) were not recorded. The distance between each egg batch and the nearest aphid was noted. Of thirty-seven egg batches, comprising a total of 526 eggs, 81 % were laid within 3·75 cm of an aphid. Eggs were present either on leaves infested with aphids or close to infested ones. Coccinellid eggs which are laid some distance from aphids or on plants bearing few or no aphids, are probably laid soon after the coccinellids have left a locality where aphids are present. For example, *A.*

bipunctata feeds on nettle aphids early in the year and then migrates to and oviposits on beans (Banks 1956). However, since individuals of the bean aphid, *Aphis fabae* Scop., do not avoid coccinellids (Dixon 1958), a fairly low population density may be high enough for the adults to capture sufficient aphids in order to mature eggs. Adults of *Adalia decempunctata* oviposit close to aphids because they

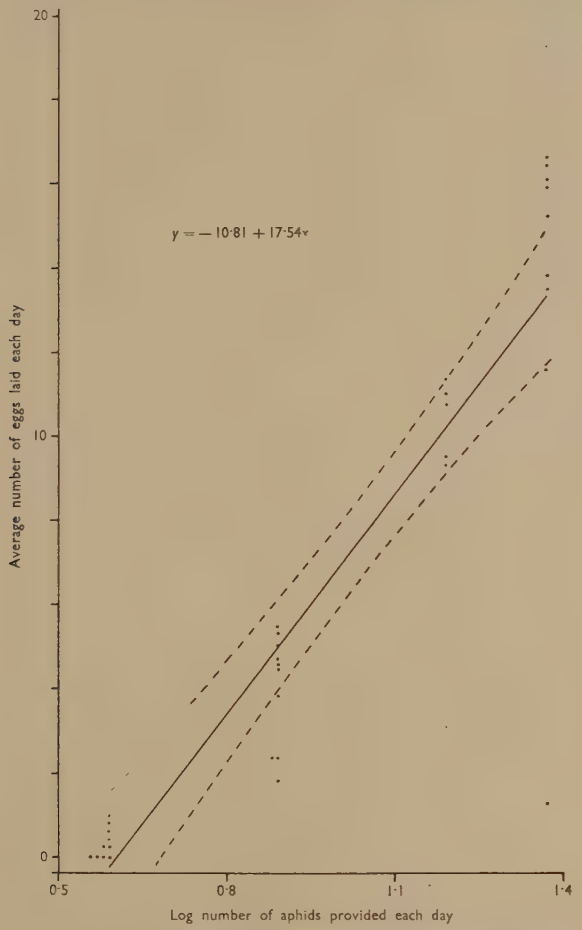

Fig. 6. The effect of the number of third-instar aphids provided each day on the number of eggs laid each day by *Adalia decempunctata*.

are less active when well fed and consequently remain in the vicinity of their own food supply. The chance that eggs will occur close to aphids is further increased since more eggs are laid when food is abundant.

As *A. decempunctata* larvae are least efficient at capturing prey in the first instar, and under favourable conditions then require a prey population density at least

twelve times greater than fourth-instar larvae for 50% survival, the relative inefficiency of the adults, when compared with later-instar larvae, may be adaptive. If the adult can capture sufficient aphids in a certain time to bring about an appreciable decrease in its activity and an increase in the rate of maturation of the eggs, the emerging larvae have a greater chance of surviving as they are more likely to emerge near dense aphid colonies. If larvae are able to survive the first instar, their chance of survival in the later instars is then relatively great since

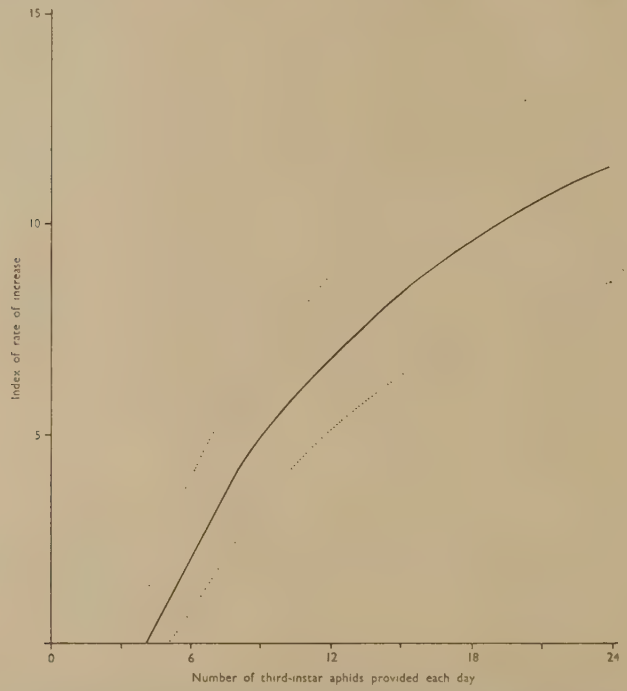

Fig. 7. The effect of the number of third-instar aphids provided each day on the index of the rate of increase of *Adalia decempunctata*. Dotted lines show the 95% fiducial limits.

they require a smaller population density for survival, and they will probably give rise to large adults. This probably accounts for the absence of small adults in the field (p. 269).

RATE OF INCREASE

The rate of increase of a speces is equal to the total number of births minus the total number of deaths in unit time. For insects which have only one generation a year, this unit of time is acceptable, and for simplicity it is assumed that *Adalia decempunctata* has only one, although in more favourable years it may have two or perhaps even three.

Assuming that irrespective of the number of aphids eaten each day, within the

range of four to twenty-four aphids, adults of *A. decempunctata* live the same length of time, then the product of the number of eggs laid each day by each female (Fig. 6) and the percentage survival of larvae when the same number of aphids is provided (Fig. 4), gives an index of the rate of increase in relation to the number of aphids provided each day (Fig. 7). Ignoring the effect of the age distribution of the prey population and assuming a random distribution of prey, as Volterra (1931) did, then the different numbers of aphids provided each day simulate the conditions at different aphid population densities. Therefore the rate of increase of *A. decempunctata* depends upon the aphid population density.

Volterra (1931, p. 415) considers that the rate of increase of a predator is linear in relation to prey population density. However, over the range of numbers of aphids provided each day there is no linear relation between the rate of increase in *A. decempunctata* and the number of aphids provided each day. Nicholson (1933) also assumes that the rate of increase of a predator population is limited by the population density of its prey. He (1933, pp. 148, 166) states: 'The number of offspring produced, though it may be influenced, is clearly not proportional to the number of prey eaten by the predator' and 'All mature predators tend to produce a surplus of offspring, so it seems clear that in the steady state this surplus must in some way be destroyed'. Thus, with increasing prey population density there would be a corresponding increase in the survival of predator offspring, for then fewer would die as a result of difficulty in finding their prey. Although Nicholson's assumption (1933) that the number of eggs produced by a predator is not proportional to the number of prey eaten is not valid for *A. decempunctata*, except at the very highest feeding rates used, his assumption that the rate of increase of a predator is limited by the prey population density applies.

DISCUSSION

Thompson (1939), Ullyett (1953), and Andrewartha & Birch (1954) have rejected Nicholson's (1933) and Volterra's (1931) assumption that animals move at random when searching for the objects they require. This is partly due to the confusion which exists through failure to notice that the term 'random' can be used in many different ways (Varley 1941). Laing (1937) states: 'A parasite finds its host, as any animal must find the things it seeks, by movements which, until they are influenced by the qualities of the object sought, are random with respect to it. When the qualities are perceived they direct the movement, which thereupon ceases to be random.' As *Adalia decempunctata* larvae or adults must touch an aphid before they respond to its presence, it can therefore be said that they move at random with respect to their prey.

As they will cross each other's tracks, individuals of *A. decempunctata* search independently of one another. Hence, also 'the searching within the population is unorganized, and therefore random' (Nicholson 1933, p. 141). In considering the term 'random search' in the sense in which it is used by Nicholson (1933), and also by Nicholson & Bailey (1935), Varley (1941, p. 48) states: 'their use of the term shows that in random search the number of encounters between predators and

prey, or parasite and host, is proportional to the product of the population densities of the two species'. Volterra (1931, p. 425) also assumes this to apply to the number of encounters between individuals of two species, one of which feeds upon the other.

It is reasonable to conclude that the responses of *A. decempunctata* adults in the laboratory would lead them to occupy and lay most of their eggs in areas where the prey population density is high in the field, and to leave these areas as soon as the prey population density fell to a certain critical minimum level. The larvae would also tend to concentrate their attack in most heavily infested areas. This behaviour would increase the effective area of search when the prey population density is low. However, Nicholson (1933, p. 171) was fully aware of a patchiness of prey distribution and consequent concentration of prey into 'groups' or 'active centres', as Elton (1949) calls them. He concluded that a polyphagous predator which concentrates its attack in areas where a species of prey is abundant would tend to damp any fluctuation in the density of the prey, and also allows a single species of predator to control the densities of a number of different species of prey simultaneously. Voûte (1943, 1946, 1951), Tinbergen (1946) and Southern (1953) cite examples of polyphagous predators concentrating their attack on a local abundance of prey and reducing it to a low level. Voûte states that such predators are usually quickly satiated, but points out that if the immigration rate is high, the predator may then be able to reduce the prey species to a low level. It has been shown that an abundance of coccinellids close to an abundance of aphids will affect immigration of these predators (Fenjves 1945, Banks 1955). The relative inefficiency of adults of *A. decempunctata* in capturing prey and their tendency to cease ovipositing and to leave an area when the return for the effort which they expend reaches a certain critical low level would save the prey from complete annihilation in that area.

The area of discovery of a species, which Nicholson (1954) subsequently called the procurement field, and applied to both parasites and predators, is not independent of the prey population density for *A. decempunctata*. Coccinellid larvae require a certain minimum number of aphids in unit time if they are to survive, and in searching for these aphids would traverse a certain area. An increase in the number of aphids available in this area would not mean a proportional increase in the number of aphids eaten, but does lead to a decrease in the length of that instar or larval stage, and consequently in the area traversed. Considering the adult coccinellid only, the first aphids eaten in excess of its minimum requirements for basic metabolism permit the maturation of eggs, but satiation soon comes into effect, and there is a maximum number of aphids which the adult can eat in a certain time and the number of eggs it can lay per unit time is limited. It is advantageous that adults should become relatively quiescent when well fed, and hence decrease the size of the area traversed, as by doing so they are likely to remain close to a relatively high concentration of their prey. Hence larvae would have a good chance of survival and no small adults would be produced. However, the population density of prey for 50% mortality varies according to the instar;

this implies that at any one time the mortality is concentrated amongst the earliest instars.

Volterra assumed that there is a linear relationship between rate of increase of a predator population and the population density of its prey. This necessitates that the predator should have an insatiable appetite. This condition does not, however, hold for *A. decempunctata*. The number of eggs laid by a predator in which the adults take the same food as the larvae is likely to be proportional to the number of prey eaten by the adult, until satiation begins to take effect. Predators in which adults take a different food from that taken by the larvae, for example, aphidophagous Syrphidae, *Leucopis* (Chamaemyiidae) and *Phaenobremia* (Cecidomyiidae), are likely to mature a number of eggs quite independent of the density of the prey that the larvae are to feed on. However, even so, not all the eggs matured are likely to be laid, irrespective of the larval prey population density. In fact, the number of eggs laid by these aphidophagous Diptera is likely to be proportional to the number of colonies found, assuming that the food supply of the adult is not a limiting factor. Hence, neither type of predator is likely to act strictly in the way outlined by Nicholson or Volterra.

Although the prey predator interaction is far more difficult to represent mathematically when the predator scrambles rather than contests for its prey (Nicholson 1954, p. 53), it is hoped that as more information becomes available on the searching behaviour of predators and the response of their prey other attempts at a mathematical formulation will be made.

ACKNOWLEDGMENTS

It is a pleasure to thank Prof. G. C. Varley for supervising this work and for his very helpful criticism of the manuscript. I also wish to thank Mr J. F. Scott for advice on statistical procedures and for the undertaking of more difficult calculations. The work was carried out while the author was in receipt of an Agricultural Research Studentship.

SUMMARY

1. A study has been made of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.).

2. Healthy eggs in a batch may hatch successively over a period of several hours. Larvae do not eat their contemporaries.

3. Of the eggs which fail to hatch when the majority of the batch does so, few would normally hatch successfully, and many are eaten by larvae which have already emerged.

4. Searching larvae are negatively geotactic and positively phototactic.

5. When searching a leaf larvae spend most time on the rim and veins.

6. Well-fed larvae tend to search an area more thoroughly than starved individuals. Starved first-instar larvae search an area more thoroughly than starved second-, third- and fourth-instar larvae do.

7. The tendency of starving fourth-instar larvae to revisit the apex of a cylinder, where there are no aphids, decreases as the period of starvation increases.

8. As larvae increase in age their efficiency in capturing the aphid *Microlophium evansi* (Theobald) increases. Larvae are more efficient in capturing young aphids. Efficiency of adults lies between that of the second- and third-instar larvae.

9. In each successive instar, the time taken to consume aphids of a particular instar decreases. Fourth-instar larvae take twelve times longer to consume an adult aphid than they do a first-instar aphid.

10. Having captured one aphid, a first-instar coccinellid larva's chance of capturing a second aphid is greater than was its chance of capturing the first.

11. The number of aphids required to be provided daily to the larvae, so that 50% survive, increases with each successive instar.

12. With increasing aphid population density, there is an increase in the rate of development and percentage survival of larvae until there are signs of satiety when approximately fifteen third-instar aphids are provided each day.

13. In each successive instar, unfed larvae are capable of covering a greater distance before succumbing to starvation. Larvae which consume very few aphids each day traverse an area greater than that traversed by those which received rather more.

14. For survival of 50% of the individuals, first-instar larvae require a prey population density many times greater than that required by fourth-instar larvae. The actual value is mainly dependent upon the age distribution of the aphid population which is being attacked.

15. Adults are less active and lay more eggs when well fed.

16. In the field, egg batches of *A. decempunctata* are usually found either on leaves infested with aphids or close to infested ones.

17. Over the range of numbers of aphids provided each day in the laboratory, there is no linear relation between the rate of increase of *A. decempunctata* and the numbers of aphids provided each day.

18. The searching ability and rate of increase of *A. decempunctata* are considered in relation to Nicholson and Volterra's assumptions, which appear oversimplified.

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THE EFFECT OF A SEWAGE EFFLUENT ON THE DISTRIBUTION OF DISSOLVED OXYGEN AND FISH IN A STREAM

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(With 5 Figures in the Text)

It is sometimes alleged that rivers are fishless below the point of discharge of a sewage effluent, and since sewage is the commonest form of pollution in this country, it is important to know whether this allegation can be substantiated and if so what factors are mainly responsible. This problem has recently been examined by Allan, Herbert & Alabaster (1958) who showed that different numbers of certain kinds of coarse fish were to be found in a channel containing undiluted sewage effluent. This channel is about a mile long, and fish were caught over its whole length in fish traps even though conditions at the down-stream end were

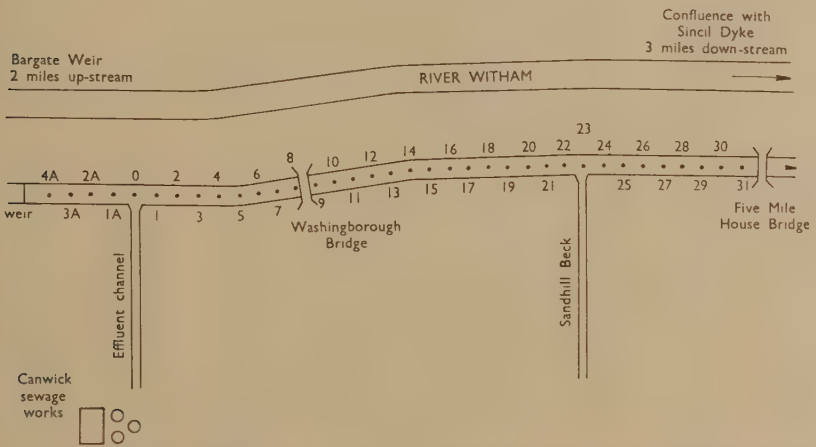

Fig. 1. Diagram of the Sincil Dyke showing (•) stations at intervals of approximately 1 furlong.

sometimes lethal both to trout and to coarse fish which were confined there in cages. However, the down-stream end of the channel was in direct communication not only with the River Colne which contained the diluted effluent, but also with the Grand Union Canal which was relatively unpolluted and which was known to contain fish. The fish in the canal thus had access to the effluent channel, and this could explain why fish were caught in traps at the lower end of the channel even when captive fish there had been killed. The authors also point out that it is possible that there would sometimes have been a fishless zone either in the effluent

channel or in the river, had there been no connection between these watercourses and the canal. Because of this possibility it was decided to make further observations at a less complicated site, and the Sincil Dyke in Lincolnshire was finally chosen.

The dyke rises from the River Witham at Bargate Weir in Lincoln, runs through the city and then in an easterly direction on a fairly straight course for about 9

Table 1. *Properties of the Canwick sewage works effluent*

Sample taken at 1400 h, 22 October 1956

Property	Concentration	Property	Concentration
Organic carbon	24·0 p.p.m.	Monohydric phenols	0·7 p.p.m.
Suspended solids	38·0 ,,	Cyanide	0·04 ,,
5-day B.O.D. (as O_2)	19·0 ,,	Thiocyanate	0·025 ,,
Permanganate value	22·0 ,,	Iron	1·2 ,,
Ammonia (as N)	28·0 ,,	Copper	0·15 ,,
Nitrite (as N)	1·0 ,,	Nickel	0·05 ,,
Nitrate (as N)	55·0 ,,	Zinc	0·20 ,,
Organic matter in suspended solids	74·0%	Lead	0·02 ,,
pH value	6·9	Chromium	0·02 ,,
Synthetic detergents (as Manoxol)	4·5 p.p.m.	Manganese	trace
Total phenols (as C_6H_5OH)	5·0 ,,		

Samples taken over a 24 h period, 14-15 November 1956

	Monohydric phenols (p.p.m. C_6H_5OH)	Total phenols (p.p.m. C_6H_5OH)	Detergents (p.p.m. Manoxol)	Thiocyanate (p.p.m. CNS)	Cyanide (p.p.m. HCN)	Ammonia (p.p.m. N)	Free CO_2 (p.p.m.
14 Nov.							
4.00 p.m.	1·0	6·0	10·0	0·37	0·02	99	7·5
5.00 ,,	1·2	6·2	9·8	0·40	nil	97	7·6
6.10 ,,	1·2	8·5	8·2	0·45	0·02	95	7·55
7.15 ,,	0·6	7·0	10·0	0·60	nil	81	5·5
8.30 ,,	1·1	8·0	7·7	0·87	nil	85	7·0
10.00 ,,	1·0	5·2	9·0	1·90	nil	82	3·7
11.20 ,,	0·8	4·8	9·0	2·80	0·03	87	4·0
15 Nov.							
12.45 a.m.	1·0	6·5	8·2	3·00	0·05	82	3·7
2.15 ,,	1·0	6·5	8·2	3·00	0·05	79	3·2
4.20 ,,	1·5	7·0	6·5	2·26	0·02	82	25
5.45 ,,	1·6	7·0	6·5	2·12	nil	82	25
7.00 ,,	1·6	7·5	7·0	2·12	0·01	85	13
8.10 ,,	2·0	8·0	7·8	2·12	0·01	99	12
9.15 ,,	1·0	6·0	8·0	2·36	nil	99	9·0
10.20 ,,	1·2	7·0	7·6	2·40	nil	99	9·8
12.00 noon	1·6	7·4	6·8	2·50	nil	103	10
1.20 p.m.	1·2	7·0	7·5	2·50	nil	107	14
2.45 ,,	1·0	5·8	7·0	2·00	0·02	107	11
4.00 ,,	1·0	5·8	7·6	2·26	nil	107	9·5

miles before rejoining the main river again just above Bardney. The Witham continues down-stream of Bardney for about 20 miles and enters the sea through sluice gates at Boston. The effluent from the Canwick sewage works, which treats the sewage from the city of Lincoln, goes into the dyke at a point about $2\frac{1}{2}$ miles from Bargate Weir, and in addition there are small discharges of drainage water all along the dyke, the most important of which enters from Sandhill Beck, about

3 miles down-stream of the effluent outfall. At the time of the survey (31 August to 7 September 1956) the height of Bargate Weir was temporarily increased to prevent the entry of any water from the main river, and since the flow over the weir was normally the main source of dilution water for the effluent in the dyke, the stoppage resulted in the dyke holding almost undiluted sewage effluent for several miles and provided an opportunity to study some of the worst conditions which might ever be expected to occur in a small stream receiving a sewage effluent.

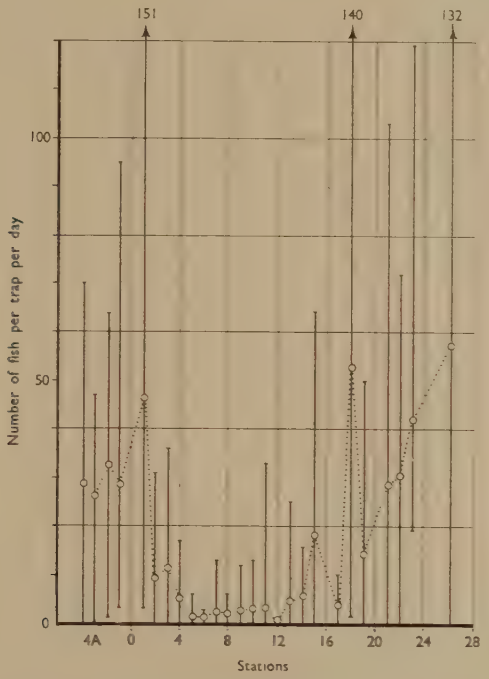

Fig. 2. Distribution of the catch of fish in the Sincil Dyke. The mean catch and the highest and lowest values are shown for each station.

The portion of the dyke in which observations were made is shown diagrammatically in Fig. 1, the width of the watercourse being considerably exaggerated. The dyke is a channel of very regular shape and all the way down to Station 6 is about 30 ft wide. Between this station and Station 10 the width gradually increases to about 40 ft and then remains roughly the same all the way down to Station 31. The depth depends largely upon the level of the River Witham at Boston, but during periods of low flow and when the tidal gates at Boston are closed it is fairly constant, being 2 or 3 ft between Station 4A and 8, and between 6 and 8 ft below Station 9. These were the depths during the survey, for there was no water coming over Bargate Weir, and the flow of effluent and the flow of the Sandhill Beck were

each estimated at about 4 million gallons per day. Chemical analyses of the effluent are given in Table 1.

METHOD

Stations were sited at furlong intervals along the dyke, numbers 4A to 1A being above the effluent outfall and numbers 1 to 31 below. On the first two days of the survey unbaited fish traps as described by Allan, Herbert & Alabaster (1958) were placed in pairs in the dyke at Stations 1A to 11, and further down-stream at

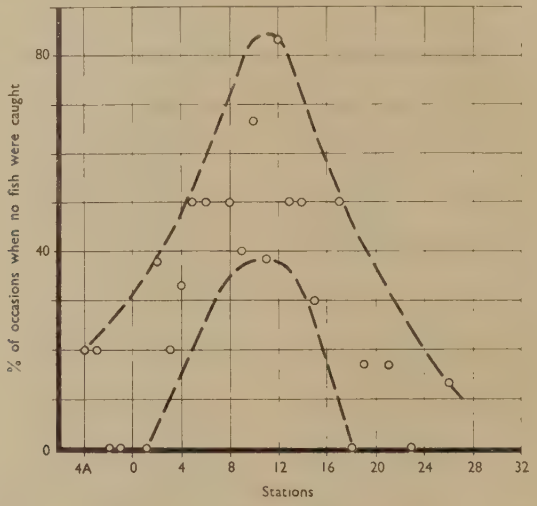

Fig. 3. Proportion of occasions when nil catches were made in traps in the Sincil Dyke.

stations ½ mile apart to Station 26. For the rest of the period single traps were placed in the dyke at most stations from Station 4A ½ mile above the effluent outfall to Station 26 nearly 3½ miles below it, that is at intervals of ⅛ mile. The traps were inspected once a day on eight successive days and on each occasion the catch was recorded, removed from the trap and returned to the dyke. At the same time a sample of the water was taken for the immediate determination of dissolved oxygen concentration and temperature.

RESULTS

(*a*) *Number of fish caught in traps*

The total number of fish caught at all stations over the whole period was 3079, of which the majority were roach. Only 52 (1·7%) were perch, and there were also in the catch 3 gudgeon, 2 eels, a bream, a pike and a dace.

The general distribution of the catch over the length of the dyke during the whole period of the survey is shown in Fig. 2 in which the average catch for each

station is plotted as a point and the highest and lowest values which were observed at each station are joined by vertical lines. While there is a considerable scatter of data, catches at Stations 4A to 1 and at stations more than $2\frac{1}{2}$ miles down-stream of the effluent outfall were generally much higher than those at the intermediate stations. Although there were no stations at which fish were never caught, there were some stations where the proportion of days on which no fish were caught was very high. The distribution of these occasions throughout the river is shown in Fig. 3, from which it is clear that the proportion is highest at stations about a mile below the effluent outfall. Where the proportion of zero catches is high it might be expected that the average catch will be lower than elsewhere, but if the data are examined by calculating the average catch per station only for days when

Table 2. *Roach mortality in traps in the Sincil Dyke*

Date	Station	Number of roach found in traps		Dissolved oxygen (p.p.m.)
		dead	alive	
31 Aug. 56	9	1	0	0·6
1 Sept. 56	9	12	0	1·6
	11	1	1	1·9
4 Sept. 56	4	1	2	1·8
	13	1	0	2·8
	14	1	0	2·3
	15	3	5	2·9
	17	10	0	2·8
	22	6	0	2·7
	23	23	0	4·2

some fish were caught, the averages are still lower for stations about 1 mile below the effluent outfall than elsewhere. Thus the low average catch in this region was attributable to a high proportion of nil catches and to a small number of fish being caught on those occasions when catches were made.

The vertical lines in Fig. 2 show that there is a wide range in the number of fish caught at any one station, but there does not appear to be any significant trend with time in the number caught during the survey. The average number caught per trap in the whole of the dyke on successive days was 35, 10, 9, 13, 21, 9, 20 and 11, and it may be that such variation is a function of the trapping method. There were, however, well-marked day-to-day variations in the extent of the zone in which no fish were caught. The trapping records for individual days show this zone extending for 0·25, 0, 1·38, 0·75, 1·13, 0 and 0·63 miles on successive days, and show that sometimes the zone existed where high numbers of fish had been caught the day before, and also that the catches could be restored within a day or so in areas where nil catches had previously been made.

Although the number of perch caught was small, there was a tendency for more to be caught at stations above the effluent outfall and at those at the lower end of the dyke than at those a few miles below the outfall. Grouping the results from Stations 4A to 1A, 1 to 6, 7 to 18 and 19 to 26, the number of perch caught during

the whole period was 7, 2, 1 and 42 for the four sections respectively, the difference being highly significant by the χ^2 test ($P < 0{\cdot}001$).

(*b*) *Fish mortalities*

On several occasions when traps were examined some of the fish found in them were dead. Details of the mortalities are given in Table 2 together with the dissolved oxygen concentration which was found at the time the traps were examined. The catch always consisted entirely of roach on these occasions, and in most cases all the fish were dead. The results demonstrate that conditions in

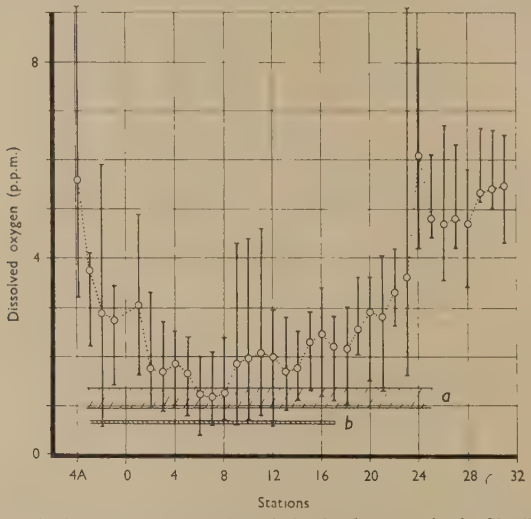

Fig. 4. Average concentration of dissolved oxygen in the Sincil Dyke. The mean concentration and the highest and lowest values are shown for each station. The width of the hatched areas *a* and *b* represent for perch and roach respectively the range of lowest dissolved oxygen concentration in which all individuals survive and the highest concentration in which they all die within a period of 3½ days (Downing & Merkens 1957).

parts of the dyke were sometimes lethal to a high proportion of captive roach within 24 h; yet there were no occasions when fish were seen dead or dying except in traps.

(*c*) *Dissolved oxygen*

The average and range of concentration of dissolved oxygen at each station over the whole period of the survey are shown in Fig. 4 and although the distribution is an irregular one, there is a marked sag curve with the minimum value occurring about 1 mile below the effluent outfall. There is also wide variation in the oxygen concentration observed at any one station which could presumably be accounted for by the variation in flow, in the quantity of oxidized matter discharged and in the time of sampling, and also, in the case of stations near Sandhill Beck, by the incomplete mixing of the side stream with the effluent.

In the same figure are shown the approximate concentrations of dissolved oxygen which have been found in laboratory experiments (Downing & Merkens 1957) to correspond with a 100% kill and 100% survival of roach and perch for a period of $3\frac{1}{2}$ days. It can be seen that the dissolved oxygen concentration in the Sincil Dyke was sometimes within these limits for both species although the number of stations at which it was within the limits for perch is very much higher than it was for roach.

(*d*) *Temperature*

The water temperature was measured whenever samples were taken for determining the dissolved oxygen concentration. The mean temperature for the whole period at all stations was $14{\cdot}5 \pm 1{\cdot}5°$ C. There was a slight tendency for the tem-

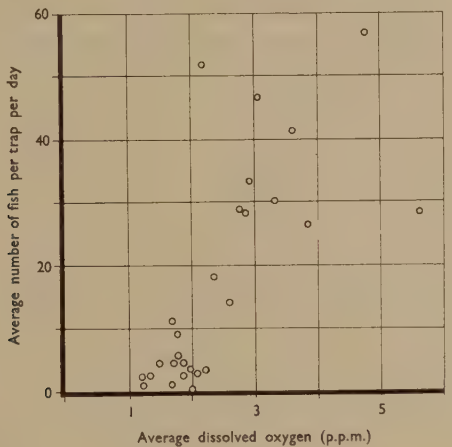

Fig. 5. Relation between the average dissolved oxygen concentration and the average catch of fish per trap per day at each station in the Sincil Dyke.

perature of the water to fall (about $0{\cdot}5°$ C) as it flowed down-stream from Station 1 to Station 31, but there was no marked trend in temperature from day to day, and there appeared to be no correlation between temperature and the number of fish caught in traps.

(*e*) *The relation between dissolved oxygen concentration and the number of fish caught*

Although the number of fish caught and the dissolved oxygen concentration varied from time to time and from station to station they bear a general similarity in distribution to each other in the dyke. A regression of the catch of fish per trap at each station on the dissolved oxygen concentration found when the traps were examined shows that the relationship between the two is highly significant ($P < 0{\cdot}001$) the catch increasing with increase in concentration of dissolved oxygen. This is also illustrated in Fig. 5 in which the average number of fish caught in traps

at each station is plotted against the average concentration of dissolved oxygen at each station.

DISCUSSION

In fishery studies the most important consequence of pollution of a river by sewage effluent is usually the reduction of the dissolved oxygen concentration, which may proceed to a value which is of itself lethal to fish or to one which markedly increases the toxicity to fish of poisons which may be present. In this survey the determination of the dissolved oxygen concentration of samples taken once a day at each station was intended only as a rough guide to the quality of the water, and undoubtedly the concentration would have changed between sampling times. Furthermore, other substances present in the effluent (Table 1) may have been present during the survey in toxic concentration. It must also be pointed out that the number of fish caught in a trap does not necessarily reflect in strict proportionality the number present in the dyke. The fish get caught in the traps by swimming into them voluntarily, and so factors which affect the fish's behaviour must also affect their chances of being caught in the traps; those which, for instance, increase the activity of the fish are likely to increase the proportion of the fish caught.

Recently Tompkins & Bridges (1958) have reported increases in the number of fish caught in fyke-nets following the application of copper sulphate to the water to give non-toxic concentrations, and they suggest that it was because of an increased activity of the fish. Similar results have been found by Mr B. Stott (personal communication) using traps identical to those used in the Sincil Dyke. Changes in other chemical or physical conditions of the water might also affect the chances of fish being trapped, but the author is not aware of any published work which shows this, although the laboratory experiments of Jones (1952) showed that fish tended to remain at rest for longer periods in water of high dissolved oxygen concentration than in water low in oxygen, when given a choice in a small aquarium. If the same is true in a river where the spatial differences in dissolved oxygen to which the fish are exposed are smaller, and if the activity of the fish is an important factor in bringing about their capture in traps, then the proportion of the population caught in traps is likely to be smaller where the dissolved oxygen concentration is high than where it is low. In the Sincil Dyke the lowest catches occurred where the oxygen was low, which suggests that there really were fewer fish in the region of low oxygen concentration than elsewhere. When using traps in an enclosed water known to contain fish it is not unusual to find empty traps occasionally (Mr B. Stott, personal communication), and similar results have been obtained by the author when trapping in rivers. In the Sincil Dyke, however, there were often a number of adjacent traps which were empty, which suggests that the results were not fortuitous and that there really was a shortage or an absence of fish in parts of the dyke. If this is true, the fact that the extent and position of the zone in which no fish were caught varied considerably from day to day suggests that the fish were moving up and down the dyke a great deal. Although one cannot expect to draw rigorous quantitative conclusions from

the data, it does appear from Fig. 5 that very few fish occur where the average dissolved oxygen concentration is less than 1 or 2 p.p.m.

Conditions in the dyke were sometimes lethal to roach, but it seems that these conditions were successfully avoided by the free-living fish, since dead fish were not found except in traps. The water in the 'fishless zone' may always have been lethal to roach even though this was not always demonstrated, and this may always have been the reason for their absence. On the other hand, conditions may not always have been lethal, but as the experiments of Hogland (1951) show that roach tend to avoid low but not lethal concentrations of dissolved oxygen when offered a choice in a gradient of dissolved oxygen, the concentration in the dyke may still have been low enough to influence the distribution of the fish.

The observations made in the Sincil Dyke confirm those made in the effluent channel leading into the River Colne that fish will live in undiluted sewage effluent provided the concentration of dissolved oxygen is high. In addition, the Sincil Dyke appeared to be fishless in the region of lowest dissolved oxygen concentration and it seems highly probable that a fishless zone would have existed in the effluent channel leading into the River Colne or in the Colne itself, had the reservoir of fish not been available in the Grand Union Canal. From this it might also be supposed that, had the dissolved oxygen always been high during the survey of the Sincil Dyke fish would have been present throughout its length.

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SUMMARY

1. Observations made in the Sincil Dyke indicate that fish will live in undiluted sewage effluent provided the concentration of dissolved oxygen is high.

2. The Sincil Dyke appeared to be fishless in the region of lowest dissolved oxygen concentration.

3. It is suggested that had the dissolved oxygen always been high during the survey of the dyke, fish would have been present throughout its length.

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ESTIMATES OF LENGTH OF LARVAL LIFE IN THREE SPECIES OF LAMPREY FOUND IN BRITAIN

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All previous attempts to estimate the length of larval life of lampreys have involved ammocoetes of brook lampreys only. Knowles (1941) estimated a larval life of 3 years, Schultze (1930) placed the figure at between 3 and 4 years, while Ivanova-Berg (1931) came to the conclusion that brook lampreys metamorphose after 5 years. Hardisty (1944) also estimated an ammocoete life span of 5 years in *Lampetra planeri* (Bloch). Hardisty (1951) mentions the possibility that the larval life of *L. planeri* might vary slightly according to environmental conditions. For this reason the author has included yet another analysis of *L. planeri* year-classes along with the completely new study of *L. fluviatilis* (L.) and *Petromyzon marinus* L. ammocoetes included in the present paper.

Ammocoetes were collected from various rivers and streams in order to obtain pure samples of each of the three species. Since the methods employed in identifying the ammocoetes (MacDonald, in press) had not been perfected when this experiment was started, all mixed samples were rejected. Large-scale collection of living ammocoetes was made possible by the generous loan of a portable D.C. electric stimulator from the Ministry of Agriculture, Fisheries and Food. Finally, three pure samples of each species were obtained, each sample having been taken at a different time of year. Ammocoetes thus taken were preserved on the spot in 4% formalin solution, and were later transferred to 70% alcohol. Length measurements were always made within a day of capture. Also, in sampling, care was taken to collect ammocoetes systematically across the river or stream concerned, as the author had reason to believe that certain age-groups of ammocoetes favour different depths of water.

RESULTS

(*a*) Lampetra planeri (*Bloch*)

Three samples of ammocoetes were taken from a small burn which enters Loch Lomond on the west side between the villages of Luss and Balloch. The three largest animals in sample A were in advanced stages of metamorphosis, the lateral eyes being open, and 'teeth' being present in the oral cavity; only the sucking disc was as yet undeveloped. In sample B two of the specimens (148 and 149 mm long respectively) had completed metamorphosis, developed open lateral eyes and a functional sucking disc possessing the proper complement of teeth. The fact, however, that they were still buried in the mud indicated that they were

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not quite ready for adult life. In sample C the largest specimen had partly opened lateral eyes and a few 'teeth' indicating that it was beginning to metamorphose.

Analysis of these samples shows that provided all metamorphosing ammocoetes are considered separately, they fall into five well-defined groups or size-classes, which do not overlap. The data are presented in Table 1, the samples being listed in order of their occurrence after the spring spawning, which the author has observed to take place in April.

Considering sample C (Table 1), since brook lampreys spawn in April, it is fair to assume that ammocoetes of size-class 1 hatched 3 or 4 months before their capture,

Table 1. *Size-classes derived from three samples of ammocoetes of* Lampetra planeri

All length measurements are ±1 mm.

Sample	Size-class	Length (mm) Range	Length (mm) Average	Number of specimens
C 30 July 1958	1	15- 21	17·4	22
	2	50- 81	69·1	10
	3	101-105	103·9	6
	4	116-140	127·3	9
	5	–	168	1
			Total	48
A 3 December 1957	1	36- 41	38·0	4
	2	–	67	1
	3	–	118	1
	4	129-155	140·4	14
	5	170-173	171·3	3
			Total	23
B 19 February 1958	1	34- 37	35·5	4
	2	71- 81	79·6	9
	3	118-123	120·4	5
	4	136-159	148·1	14
	5	148-149	148·5	2
			Total	34

that size-class 2 ammocoetes were a year older, and so forth. That is, since lampreys only spawn once a year, every size-class can in reality be considered as a year-class. This would indicate that the larval life of *L. planeri* lasts more than 4 years, but less than 5. Analysis of sample A lends strength to this view, because in the 4-month interim separating it from sample C, the ammocoetes of size-class 1 can be thought of as having grown an average of 20·5 mm in length from 17·5 to 38·0 mm. This, of course, assumes that the length of larval life of any one species of ammocoete never varies by more than a few months.

Comparison of samples A and B gives the impression that little if any linear growth takes place in larvae during the winter months; Hardisty (1944) came to the same conclusion. The two metamorphosed ammocoetes of sample B were

smaller than some of those ammocoetes of size-class 4 in the same sample. Vladykov (1949), Schultze (1930) and many others have stated that newly metamorphosed adult lampreys are somewhat smaller than many ammocoetes of the same species. The shrinkage during metamorphosis is thought to be due in part to the fact that ammocoetes do not feed during this period of change.

(*b*) Lampetra fluviatilis (*L.*)

Three pure samples of river lamprey ammocoetes were taken from the Fruin River, which enters Loch Lomond approximately 1 km west of the burn wherein

Table 2. *Size classes derived from three samples of ammocoetes of* Lampetra fluviatilis

All length measurements are ±1 mm.

Sample	Size-class	Length (mm) Range	Length (mm) Average	Number of specimens
C 20 June 1958	1	11- 14	12·7	3
	2	43- 69	56·4	25
	3	80- 88	84·3	10
	4	113-120	116·6	8
	5	149-158	154·2	9
	6	185-188	186·3	3
			Total	58
A 5 November 1957	1	23- 31	26·0	6
	2	58- 65	61·0	7
	3	87- 89	88·0	3
	4	128-133	130·4	5
	5	159-161	160·0	3
	6	195-198	196·5	5
			Total	29
B 23 February 1958	1	24- 29	26·3	7
	2	53- 59	56·9	11
	3	–	86	1
	4	157-159	158·6	7
	5	171-176	173·0	5
	6	130-131	130·5	2
			Total	33

were obtained the brook lamprey larvae. The five largest animals in sample A were in advanced stages of metamorphosis, and two of the ammocoetes (130 and 131 mm in length respectively) in sample B had metamorphosed, but were still buried in the mud. The data are arranged in order of size-classes in Table 2 in the same way as was done with the data from the brook lamprey samples.

Assuming the rate of growth of ammocoetes to have been not significantly different during 1957 and 1958, and applying the same system of analysis as that used in the case of *L. planeri* ammocoetes, one arrives at the conclusion that the larval life of river lampreys lasts for slightly less than 6 years.

(*c*) Petromyzon marinus *L.*

Ammocoetes of this species were far scarcer in the areas searched than were larvae of either river or brook lampreys. Finally three pure samples were taken, however, all from the Inler Burn. This waterway is a man-made trench extending off the River Leven which enters Loch Lomond at Balloch about 2 km below the loch. Seven ammocoetes in sample A had completed metamorphosis, all possessing 'teeth', well-developed lateral eyes and functional sucking discs. The typical ammocoete colour had been replaced on two of them (228 and 239 mm long respectively) by the black dorsal surface and silvery ventral surface of the adult

Table 3. *Size-classes derived from three samples of ammocoetes of* Petromyzon marinus

All length measurements are ±1 mm.

Sample	Size-class	Length (mm.) Range	Length (mm.) Average	Number of specimens
C 2 August 1958	1	23- 38	15·3	4
	2	68- 83	73·4	5
	3	112-125	121·3	6
	4	141-155	146·8	5
	5	197-202	199·5	2
	6	250-260	254·3	3
			Total	25
A 1 December 1957	1	34- 50	40·4	12
	2	85- 87	91·0	3
	3	142-147	145·0	3
	4	186-195	192·0	5
	5	235-251	244·0	4
	6	223-239	231·7	7
			Total	34
B 15 March 1958	1	40- 43	40·9	9
	2	90- 95	92·2	5
	3	148-149	148·5	2
	4	190-194	192·6	5
	5	244-246	245·0	2
			Total	23

lamprey. However, all seven of these specimens were still buried. The three largest specimens of sample 6 were also beginning metamorphosis.

In sample A the seven metamorphosing ammocoetes should be considered as a separate size-class. Sample C (Table 3) is straightforward, indicating that sea lampreys have a larval life of between 5 and 6 years before metamorphosing. During the 5-month interim between samples A and B (assuming again that the rate of growth in ammocoetes is roughly the same each summer) considerable growth apparently takes place, except in size-class 6 animals, which seem to undergo a decrease in length. Since these latter ammocoetes were already metamorphosing, it is probably correct to associate this shrinkage with starvation. In

sample B no size-class 6 animals were evident, indicating that metamorphosis must have been completed before the date on which the sample was taken.

The currently popular practice of ascertaining the species of metamorphosing ammocoetes by their relative sizes is not accurate when river and brook lampreys are concerned. Although *Lampetra fluviatilis* remains in the larval state for a year longer than does *L. planeri*, there is not a great difference in average length of these two species during metamorphosis. Differentiation of species by length alone applies when larvae of *Petromyzon marinus* are being considered, for these are significantly larger than metamorphosing ammocoetes of either of the other two species. However, the date at which metamorphosis is completed also prevents the sea lamprey from being mistaken for either of the other two. Whereas all three species begin metamorphosis in early autumn, the sea lamprey completes the process by mid-winter, whereas newly metamorphosed river and brook lampreys do not emerge until the spring.

It seems reasonable to conclude from the data that none of the three species of ammocoete here studied undergoes any significant increase during the winter months. This strengthens the claim of Hardisty (1944) that brook lamprey ammocoetes do not feed in cold weather. Laboratory experiments at present being carried out seem to indicate that all size-classes actually shrink somewhat in winter, but this requires further verification. Although the present author's estimate of length of larval life in *Lampetra planeri* is somewhat less than Hardisty's (1944) estimate, this difference is not significant.

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SUMMARY

1. *Lampetra planeri* ammocoetes metamorphose after close to 5 to 6 years of larval life, those of *L. fluviatilis* after close to 6 years, those of *Petromyzon marinus* after slightly more than 5½ years of larval life.

2. The ammocoetes of *P. marinus* commence metamorphosis in the autumn and complete it by about mid-winter; those of the other two species also begin in the autumn but do not complete metamorphosis until the following spring.

3. The ammocoetes of all three species make no increase in length during the winter months and decrease in length during the final stages of metamorphosis.

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THE DISTRIBUTION AND STATUS OF *RATTUS RATTUS* L. IN THE UNITED KINGDOM IN 1951 AND 1956

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(With 2 Figures in the Text)

The status of *Rattus rattus*, the 'ship', 'black' or 'roof' rat, in the principal sea-ports of the United Kingdom has been discussed in two papers by Matheson (1939, 1958). The earlier report was based on his experiences in Cardiff and on the answers to a questionnaire sent to the Medical Officers of Health of twenty-two sea-ports. It chiefly dealt with the pre-war trend in numbers of rats arriving in ocean-going vessels, but gave some attention to rats on land. Matheson's more recent paper re-examines the position on ships after an interval of nearly 20 years and also briefly discusses the occurrence of *R. rattus* ashore in six ports and in the City of London.

The present account is concerned solely with the distribution of ship rats living ashore. It is based on nearly 1500 replies to a questionnaire addressed to every local authority in the United Kingdom. These replies were mostly returned through Divisional Rodent Inspectors or other officers of the Ministry of Agriculture, Fisheries and Food, the Department of Agriculture for Scotland and the Northern Ireland Ministry of Health and Local Government, who checked through them in the light of their own knowledge of the localities concerned. The information supplied may therefore be regarded as being very dependable.

THE QUESTIONNAIRE

The questionnaire asked for the following information:

1. The name and description of the authority.
2. The incidence of *Rattus rattus* on land (including permanently moored vessels) during 1951 and 1956 classified under four headings: (*a*) No occurrences. (*b*) Five or less infestations identified. (*c*) More than five infestations identified, but ship rats not thought to be always present. (*d*) Ship rats always present somewhere in the area.
3. Whether there had been any alteration (not covered by Question 2) in the frequency of ship rat infestations between 1951 and 1956, and on what kind of information the reply was based.
4. Whether the range of *R. rattus* had altered since 1951, indicating the reply by a rough map, if possible.
5. The greatest distance from waterside berths or waterside commercial buildings at which ship rats commonly occur.
6. The reasons for any change noted in the status of *R. rattus* (in range or numbers) in recent years.
7. The percentage of rat infestations investigated that were ascribed to *R. rattus* rather than to *R. norvegicus* in 1951 and 1956.

The years 1956 and 1951 were chosen for attention because the inquiry was conducted in 1957 and because it was thought that information based on records older than about 5 years would not be very reliable. It was realized that the answers to Question 7 would be of little statistical use without data also on the incidence of *R. norvegicus* in 1951 and 1956. Nevertheless, the information supplied was often of value in checking the replies to the other questions.

No attempt was made in the questionnaire to distinguish between the so-called sub-species of *R. rattus*. As Fisher (1950) has pointed out, in Britain they are best regarded as polymorphic forms of a single species. In passing, however, it may be noted that though Matheson was informed at the time of his 1939 survey that the form referred to as '*R.r. frugivorus*' was less common in London than '*R.r. alexandrinus*', my own observations agree with those of Watson (1950) who found a greater proportion of the white-bellied form (*R.r. frugivorus*) in the 4000 odd ship rats examined by him in 1942. Of 538 rats caught for me on land in London since 1950, 70% have been white- or cream-bellied and only 3% referable to the *alexandrinus* form.

RESULTS

(*a*) *The position in 1951*

As expected, most local authorities reported the complete absence of *Rattus rattus* in both 1951 and 1956; only about ninety positive returns were received. Of these, perhaps most interest attaches to places (see Fig. 1) where the ship rat was sufficiently well established to be reported as 'always present somewhere'. In 1951 in England and Wales they were as follows:

Newcastle (1)*	Bermondsey	Westminster	Sharpness (21)
South Shields (2)	Finsbury	West Ham	Gloucester (22)
Hartlepool (3)	Fulham	Ware (10)	Cardiff (23)
Middlesbrough (4)	Greenwich	Enfield (11)	Swansea (24)
Hull (5)	Holborn	Slough (12)	Wallasey (25)
Gt Yarmouth (6)	City of London	Erith (13)	Liverpool (26)
Ipswich (7)	Poplar	Chatham (14)	Bootle (27)
Maldon (8)	St Marylebone	Ramsgate (15)	Urmston (28)
The Port of London (including Tilbury Docks) (9)	St Pancras	Portsmouth (16)	Stretford (29)
	Shoreditch	Southampton (17)	Salford (30)
	Southwark	Falmouth (18)	Preston (31)
Battersea	Stepney	Penzance (19)	Barrow-in-Furness (32)
Bethnal Green	Wandsworth	Bristol & Avonmouth (20)	

In Scotland they were:

Stornoway (33)	Aberdeen (35)	Edinburgh and Leith (37)	Clydebank (39)
Lerwick (34)	Dundee (36)	Glasgow (38)	Dumbarton (40)

In Northern Ireland they were:

Belfast (41)	Londonderry (42)

Inclusion of an authority in the above list does not mean, however, that *R. rattus* was either common or widely distributed. Leaving out of consideration the London area, which will be discussed separately below, the following places reported that though the ship rat was always present, five or less infestations were located in 1951: Ipswich, Maldon, Ware, Enfield, Erith, Falmouth and Clydebank. Falmouth is included on the strength of a single persistent infestation.

* The numbers in parentheses refer to locations on Fig. 1.

Fig. 1. Distribution of 'established' populations of *R. rattus* in the United Kingdom in 1951 (dots and open circles) and in 1956 (dots only).

Twelve more authorities stated that the ship rat was restricted to dock or harbour property. These were: South Shields, Hull, Chatham, Portsmouth, Southampton, Sharpness, Wallasey, Salford, Preston, Dundee, Glasgow and Dumbarton.

In the following ports, outside the immediate confines of the docks, harbour or riverside, the footing of the species in 1951 would seem to have been precarious: Middlesbrough, Hartlepool, Hull (?), Gt Yarmouth, Ramsgate, Penzance, Gloucester, Swansea, Bootle, Urmston and Londonderry. Indeed, *R. rattus* seemed in 1951 to be reasonably well entrenched in buildings outside the dock area only at: Bristol and Avonmouth, Cardiff, Liverpool, Stretford (Trafford Park), Barrow-in-Furness, Stornoway, Lerwick, Edinburgh and perhaps Belfast. Bristol and Liverpool probably harboured larger populations than anywhere else in the United Kingdom outside London.

The occurrence of *R. rattus* in Slough might not be expected. About twelve infestations were recorded in 1951. However, all were located on the Trading Estate, which is linked to London by the Grand Union Canal and attracts a considerable weight of road traffic. There is evidence to show that the *R. rattus* population in Ware is supplemented from time to time by individuals brought from London Docks by barge up the River Lea. The same waterway explains the presence of ship rats in Enfield.

The localities outside London where the ship rat was not thought to be permanently established in 1951, but where more than five infestations were identified, are only five in number: Sunderland (probably), Stockton, Plymouth, Ellesmere Port and Fleetwood. Presumably conditions for reinfestation from vessels were present in these ports and only persistent control measures were keeping them off the list of places where *R. rattus* was always present.

In 1951, omitting Ipswich, Maldon, Ware, Enfield, Erith, Falmouth and Clydebank, which have been mentioned already, five or less than five infestations were reported by seventeen local authorities: Eston (Tees), Thornaby (Tees), Parkeston Quay, Brentford and Chiswick, Dartford, Chatham (outside the Dockyard), Dover, Poole, Brixham, Stoke, Birkenhead ('few'), Isle of Man, St. Helens, Brighouse (Yorks.), County of Ayr (excluding Ayr and Kilmarnock Boroughs), County of Renfrew and Kirkcaldy. Most of these localities probably saw at least a few ships rats before 1951. The exceptions were Brighouse, where only one infestation, cleared in 1952, was concerned, Stoke and St Helens. These are each included because of two very minor occurrences, probably road-borne. A few such isolated reports of *R. rattus* from inland towns are reported every year.

In London *R. rattus* is more widely spread than elsewhere in the United Kingdom. Its activities in the West End have been referred to in a short note by Fisher (1950) who also listed several metropolitan authorities (and other adjacent authorities) from within whose boundaries it has been reported. The only Metropolitan Borough conspicuously absent from Fisher's list is Bethnal Green, where it is very probable that a few ship rats were established in 1949. The position in 1951 was roughly as shown in Fig. 2. *R. rattus* was established in all the riparian boroughs to the south of the Thames from Erith westwards to Wandsworth, with

the exception of Deptford, which has a very short frontage on the river, and Lambeth, where, however, several infestations occurred during the year. Ship rats were also to be found in Camberwell, mostly in the vicinity of the Surrey Canal. However, it is noteworthy that no local authority on the south bank reported the presence of the species very far inland. Its restriction to riverside buildings was particularly marked in the cases of Wandsworth, Battersea and Lambeth, while in Southwark, for example, it only occurred to the north of the Elephant and Castle.

The position to the north of the Thames in 1951 was rather different. Not only was *R. rattus* ever present in the several docks (including Tilbury) under the jurisdiction of the London Port Health Authority and within the boundaries of

Fig. 2. Approximate distribution of *R. rattus* in and near London in 1951. Key to authorities:

1, City of London	10, Hackney	18, Brentford & Chiswick	26, Lewisham
2, Holborn	11, Stoke Newington	19, Wandsworth	27, Greenwich
3, Westminster	12, Hampstead	20, Battersea	28, Woolwich
4, St Marylebone	13, Paddington	21, Lambeth	29, Erith
5, St Pancras	14, Kensington	22, Southwark	30, East Ham
6, Finsbury	15, Chelsea	23, Camberwell	31, West Ham
7, Islington	16, Fulham	24, Bermondsey	32, Poplar
8, Shoreditch	17, Hammersmith	25, Deptford	33, Stepney
9, Bethnal Green			

every riparian authority from West Ham westwards to Fulham (Chelsea excepted), but it was established throughout Holborn, St Marylebone and Finsbury (chiefly in the southern half). It was also present in Islington, in Shoreditch (in a ½ mile strip to the north of the southern boundary) and in the south-western corner of Bethnal Green (adjoining Shoreditch and Stepney). Eastwards of the City of London, *R. rattus* was again more or less restricted to the river in 1951. In Stepney it occurred only on or near the riverside and in one small area adjoining Shoreditch, while in Poplar it was confined to the Isle of Dogs. In West Ham it was found mainly in river or canal-side buildings. In East Ham only 'five or less' infestations were identified in 1951. It would thus seem that Central London provides certain conditions favourable for the establishment of *R. rattus* that are

not to be found further eastwards or to the south of the Thames. There is little doubt that these conditions are the presence of numerous, multi-storied, centrally heated, and, particularly, non-residential, buildings interspersed with restaurants, canteens and other sources of food.

(*b*) *The position in 1956*

It seems quite clear that over the United Kingdom as a whole ship rats declined in range and numbers in the 5 years after 1951. In only three places where *R. rattus* was established in 1951 had an increase in its numbers been observed by 1956. These were Finsbury, Bristol and Dundee. No change in numbers was reported from Hull, Maldon, Ware, Battersea, Fulham, Wallasey and Clydebank, while Bootle and Salford were unable to give an opinion. Every one of the remaining forty-seven local authorities concerned reported a decrease.

Fig. 1 shows that not only had the ship rat failed to establish itself in 1956 in any place where it had been absent in 1951, but in thirteen localities it had lost its permanent foothold: South Shields, Gt Yarmouth, Ipswich, Bethnal Green, St Marylebone, Enfield, Slough, Erith, Ramsgate, Falmouth, Swansea, Preston and Londonderry. No infestations at all were reported in 1956 from Gt Yarmouth, Ipswich, Enfield, Erith, Falmouth and Preston. Only one was reported from Ramsgate, two from Slough and five or less from South Shields, Swansea and Londonderry.

At Hartlepool the ship rat was still to be found in 1956 on the docks but no longer outside them, while at Urmston, though it was still reported to be 'always present', only five or less infestations were noted. Of the five ports where *R. rattus* was not permanently ensconced in 1951, but where more than five infestations had been reported, one, Stockton-on-Tees, reported its absence in 1956, while Sunderland, Plymouth, Ellesmere Port and Fleetwood noted less than five infestations.

Of the seventeen authorities (Ipswich, etc., excepted) where five or less infestations were known in 1951, only Eston, Brixham and Birkenhead reported *R. rattus* in 1956. It was thus no longer recorded from: Thornaby, Parkeston Quay, Brentford and Chiswick, Dartford, Chatham (outside the R.N. Dockyard), Dover, Poole, Stoke, Isle of Man, St Helens, Brighouse, County of Ayr, County of Renfrew and Kirkcaldy. This surrender of territory was in no way counterbalanced by the unexpected appearance of the ship rat on a single occasion at each of the following places, since it appears to have been eliminated immediately: Northfleet, Swindon, Trowbridge, Fulwood (Lancs.), Ayr (Burgh) and Greenock.

The pattern of the changes in the status of the ship rat in London between 1951 and 1956 resembles that for Britain as a whole. Only two Metropolitan boroughs, Shoreditch and Finsbury, reported an increase in the range of the species. In Shoreditch, *R. rattus* seemed to have declined in numbers by 1956 but infestations were more diffuse, extending throughout the borough. In Finsbury the ship rat appeared to be both slightly more numerous and more widespread, but this

impression may have been merely the result of more inspections. It was suggested that, if the extension of range were real, it could have come about by the disturbance of old-established colonies during demolition work.

Only two authorities, Battersea and Fulham, noted no alteration in the position by 1956. The majority reported fewer *R. rattus* infestations though little or no change in their distribution. They were: Port of London (including Tilbury Docks), Westminster, City of London, Holborn, Bethnal Green, Stepney, Poplar, West Ham, Greenwich, Camberwell, Southwark and Lambeth. In the Port of London, infestations in warehouses and in batteries of moored barges were said not only to be fewer but smaller. This is borne out by the number of *R. rattus* bodies recovered in control operations in 1951 and 1956—3220 and 1123 respectively (Morgan 1952, Greenwood Wilson 1957, Matheson 1958).

A reduction in both numbers and range was reported by: St Marylebone, St Pancras, Islington, East Ham, Woolwich, Bermondsey and Wandsworth. No details are available for St Marylebone and Wandsworth, except that in the former borough, *R. rattus* was no longer 'always present'. In St Pancras the population scattered about the area to the north-west of Euston in 1951 had gone by 1956. In Islington there were more *R. rattus* infestations reported in 1952 than in 1951, but in subsequent years the figure declined progressively. None was reported in 1956. At Woolwich and Bermondsey by that year *R. rattus* had been confined to riverside property, while East Ham was apparently quite free from ship rats.

DISCUSSION

In many parts of the world *Rattus rattus* is completely at home away from buildings. In Britain, however, presumably because of the cool climate, it is an indoor animal. In ports where large blocks of multi-storied buildings are frequent, this handicap does not hinder its fairly rapid spread. But districts consisting, for example, of streets of semi-detached houses, notwithstanding any number of carelessly maintained dust-bins and chicken-runs, are a barrier to it, as are open spaces and even wide thoroughfares. To cross them it needs to be transported by man. It seems likely that this fact provides a basis for explaining the decrease in the status of *R. rattus* between 1951 and 1956.

Four other points must be made. In the first place, as the Ministry of Health (1955) and Matheson (1958) have indicated, the number of ship-borne rats arriving in United Kingdom ports is steadily declining. This follows, for instance, from a consideration of recent annual percentages of foreign-going ships inspected that have needed to be deratted. For 1951 and 1956 they were 10·07% and 6·37% for England and Wales, and 17·34% and 6·00% for Scotland, respectively. The trend towards cleaner ships is perhaps partly because more and more ports abroad are acquiring deratting facilities, but, as pointed out by the Ministry of Health, it has also largely come about because ship-designers are now very much alive to the importance of rat-proofing. Some examples of the proofing devices now being adopted have been given by the Chief Medical Officer of Health (Ministry of

Health 1955). His account ends with the remark: 'As a result of these constructional changes many modern ships have been entirely free from rats since being commissioned.'

Secondly, although there has been no obvious increase in the precautions taken to prevent the movement of rats inland by road or by rail, greater efforts have been made to reduce rat infestation in lighters and in coastal vessels of all types. By the introduction of *The Prevention of Damage by Pests (Application to Shipping) Order, 1951*, several of the requirements of the parent act of 1949 were made to apply to vessels plying only in or between places in the United Kingdom. The Order gave exemption from these requirements, however, to vessels carrying a current Rodent Control Certificate issuable by a port health authority (in England and Wales) or a port local authority (in Scotland). The implementation of this Order has undoubtedly reduced the spread of ship rats in recent years.

Thirdly, there have been improvements since 1951 in the methods of rat destruction employed by local authorities and servicing companies. In certain port health areas, notably London, where conditions of use can be carefully controlled, sodium fluoracetate has largely supplanted less acutely toxic rodenticides such as arsenic trioxide and zinc phosphide; elsewhere the introduction of chronic baiting with the so-called anticoagulant poisons has also led to better results. And though, up to the present, chronic baiting has been rather more successful against *R. norvegicus* than *R. rattus*, which is generally more resistant to anticoagulants, both species have been adversely affected, the ship rat partly because more attention has been given to it, as the common rat has been reduced in numbers.

Finally, there has been an increasing amount of new building and reconstruction of existing buildings in many ports since the war. The results of this have been to make it more difficult for *R. rattus* to gain a footing and to make the task of control easier.

The situation therefore appears to be that, in general, in the United Kingdom, *R. rattus* populations were everywhere at greater risk in 1956 than in 1951 and were less likely to be augmented by immigration. In outlying districts, such as St Marylebone, where in 1951 some ship rats were established as far away as 3 miles from harbourside warehouses, and where the population was probably maintaining itself without frequent arrivals from outside, improved control methods alone presumably accounted for the decrease in numbers. They were also probably responsible for the decrease in Central London and for the elimination of the ship rat from localities such as Stockton-on-Tees, Gt Yarmouth, Enfield, Islington and Ramsgate. At Ipswich persistent control measures and improved building construction combined to produce this result, while at Erith the reasons for the disappearance of the species by 1956 were thought to be reconstruction of buildings, change of user and the improved condition of coastal vessels consequent upon the introduction of Rodent Control Certificates. In other localities, such as the riparian boroughs of Bermondsey and Woolwich and the ports of Hartlepool, Swansea, Barrow, Glasgow, Belfast and Londonderry, where *R. rattus* was forced nearer to the waterside between 1951 and 1956, the causes were probably increased

control efficiency and a reduction in the number of rats moving out from the wharves to supplement whatever breeding was occurring in the resident population.

As far as the future status of *R. rattus* is concerned it may be surmised that during the next decade it will become uncommon in several more of the smaller ports in the United Kingdom and lose ground also in the major ports. For the trend towards cleaner ships and adequately rat-proofed warehouses is likely to continue, and at least one chronic poison that is more effective against *R. rattus* than warfarin is now known, if not yet commercially available. However, there is little likelihood of completely eliminating the species from Britain. It can be expected to persist for a considerable time yet in the commercial quarters adjacent to the docks in London, Bristol and Liverpool (and perhaps Edinburgh and Belfast) where conditions for its continued existence seem most favourable.

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SUMMARY

1. The distribution of *Rattus rattus* in the United Kingdom in 1951 and 1956 has been elucidated, mainly from the replies to a questionnaire sent to all local authorities.

2. In 1951 the ship rat was well established ashore in the London area and in about forty localities outside it, and occurred sporadically in about thirty other places.

3. By 1956 it had decreased in range and frequency in most localities and disappeared from some.

4. The main factors responsible for its loss of ground between 1951 and 1956 are thought to be the continuous reduction in the number of rats arriving in the ports in ocean-going vessels, the introduction of measures to reduce rat infestation in coastal vessels, improvements in dockside building construction, and improved methods of rat control on land.

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SEASONAL AND DIURNAL ACTIVITY OF CARABIDAE, WITH PARTICULAR REFERENCE TO *NEBRIA*, *NOTIOPHILUS* AND *FERONIA*

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(With 10 Figures in the Text)

The principal aim of this series of observations was to compare the balance of activity by night and day on the floor of contrasted habitats, and a quantitative analysis of the total fauna has already been made (Williams 1959). In a qualitative survey, pride of place must be accorded to the ground beetles for these are the most conspicuous of the floor inhabitants. Of the ground beetles, the abundant species *Nebria brevicollis* (F.), *Notiophilus* spp. and *Feronia madida* (F.) are considered in detail for they illustrate a number of points of ecological interest.

The methods of investigation, based on the use of pitfalls, have been described (Williams 1959) so may be summarized briefly. From February 1952 there was a year of sampling with simple pitfall traps 1 m in circumference. Three habitats were investigated: Rushy Mead, a deciduous wood; Mill Copse, an area of open scrub; and Mill Field, a ley newly seeded under barley which had been harvested in the autumn of 1951. In each habitat three pitfalls were sunk and these were in operation for a week at a time with an interval of 4 weeks between the start of each sample. For a year from July 1956, Rushy Mead and Mill Copse were each sampled by a trap which included a time-sorting mechanism segregating the catch into six periods, thus giving a picture of diurnal periodicity throughout the year (Williams 1958). The two traps operated simultaneously for a day at a time, sampling being at approximately fortnightly intervals.

Diurnal periodicity was also determined in Rushy Mead by quadrat counts in September 1953 and May 1954. Sixteen quadrats, each $\frac{1}{16}$ sq. m, were placed in four rows of four, each row traversing a different type of floor cover. Animals moving in the quadrat during a 10 min watch were picked out, those moving at night being observed by lamplight. Four quadrats were examined each hour, one from each row, the precise order of sampling being determined beforehand from a table of random numbers. Observations were continued for 8 h and the picture of activity during the 24 h period was built up from three sampling periods as near to each other as possible.

CARABIDAE IN GENERAL

During the year of trapping by simple pitfalls, forty-two species of carabids were caught and these are listed for the individual traps in Table 1. Rushy Mead is the habitat richest in the number and variety of ground beetles and in the number specific to a single habitat. Mill Copse is the poorest, and the intermediate position

occupied by Mill Field can be seen from Table 1 but is brought out more clearly in Table 2 where the traps and the species of beetle of which more than ten individuals were caught are arranged along the margins to show a gradation in distribution.

Table 1. *Summary of the species of carabid beetles taken in a year's sampling with simple pitfalls*

Habitat type	Wood			Scrub			Ley		
Area	Rushy Mead			Mill Copse			Mill Field		
Traps	A	B	C	A	B	C	A	B	C
Leistus ferrugineus (L.)	–	–	1	–	–	1	–	–	–
Nebria brevicollis (F.)	62	29	39	1	1	1	17	8	38
Notiophilus palustris (Duft.)	–	–	–	–	–	–	–	1	–
N. substriatus Wat.	–	2	–	–	–	1	8	1	–
N. rufipes Curt.	–	1	5	–	–		1		–
N. biguttatus (F.)	2	1	10	–	–	–	–	–	–
Loricera pilicornis (F.)	5	3	1	–		–		2	3
Clivina fossor (L.)		2	–		–	–	–	–	–
Dyschirius globosus (Hbst.)	–	3		–		–	–	–	–
Asaphidion flavipes (L.)	–		3	–	–	–		–	
Bembidion lampros (Hbst.)	–		–	1			1	–	1
B. ustulatum (L.)	–	–	1	–		–	–	–	–
B. normannum Dcj.	–		2		–	1		–	1
B. quadrimaculatum (L.)	–	–	1	–	–	–	–	–	–
B. obtusum Ser.	–	–	–	–	–	–	–	1	1
B. harpaloides Ser.	–	–	21	–	–	–	–	–	–
B. aeneum Germ.	3	–	–	–	2	–	–	–	2
B. guttula (F.)	4	–	–	–	–	3	–	–	1
Trechus obtusus Er.	1	1	5	3	2	–	–	–	3
T. secalis Pk.	–	1	–	–	–	–	–	–	–
Harpalus aeneus (F.)	–	–	–	–	–	–	2	–	2
H. rubripes (Duft.)	–	–	1	1	4	2	–	5	2
Acupalpus luridus Dej.	–	–	–	–	–	–	–	–	1
Amara communis (Pz.)	–	–	–	1	4	1	3	1	–
A. curta Dej.	–	–	–	3	9	2	–	1	
A. aenea (De G.)	–	–	–	–	–	–	–	–	1
A. familiaris (Duft.)	–	–	–	1	1	1	–	–	–
Stomis pumicatus (Pz.)	1	1	–	1	–	1	–	–	
Feronia cupraea (L.)		–	–	3	6	1	–	–	–
F. vernalis (Pz.)	1	–		1	–	–			1
F. macra (Marsh.)	–	–	–	–	–	–	–	1	–
F. melanaria (Ill.)	–	–	–	–	–	–	–	1	–
F. nigrita (F.)	1	2	5	1	–	–	–	–	–
F. gracilis (Dej.)	–	–	–	–	–	–	–	–	1
F. strenua (Pz.)	3	12	–	–	–	–	–	–	–
F. diligens Stm.	–	–	–	–	–	–	–	1	–
F. madida (F.)	4	2	14	7	8	3	1	1	1
Calathus piceus (Marsh.)	–	–	1	–	–	–	–	–	–
*Agonum müller*i (Hbst.)	–	–	1	–	–	–	–	–	–
A. viduum (Pz.)	–	–	–	–	–	–	–	–	1
A. livens (Gyll.)	–	–	1	–	–	–	–		
A. dorsale (Pont.)	–	–	–	–	–	–	–	–	1

The trap sequence of Table 2 is a series representing a decreasing proportion of litter on the ground; Rushy Mead trap C is in pure hawthorn litter with no ground flora, RM A and RM B are under oak and alder respectively with progressive development of a ground flora and reduction of litter, Mill Field trap C is adjacent

to a hawthorn hedge and lies in a narrow strip of litter, while MF B and MF A are progressively farther removed from the boundary hedge. The paucity of the carabid fauna in Mill Copse is probably due to the fact that this area is completely uncultivated, and it is a common observation that such neglected open ground

Table 2. *The twelve commonest species of carabid arranged to illustrate a sequence of distribution of the traps*

RM, Rushy Mead; MF, Mill Field; MC, Mill Copse

	Traps								
	RM C	RM A	RM B	MF C	MF B	MF A	MC C	MC A	MC B
Bembidion harpaloides	21	–	–	–	–	–	–	–	–
Notiophilus biguttatus	10	2	1	–	–		–	–	–
Feronia strenua	–	3	12	–	–	–	–	–	–
Loricera pilicornis	1	5	3	3	2	–	–	–	–
Nebria brevicollis	39	62	29	38	8	17	1	1	1
Feronia madida	14	4	2	1	1	1	3	7	8
Trechus obtusus	5	1	1	3	–	–	–	3	2
Notiophilus substriatus	–	–	2	–	1	8	1	–	–
Harpalus rubripes	1	–	–	2	5	–	2	1	4
Amara communis	–	–	–	–	1	3	1	1	4
A. curta	–	–	–	–	1	–	2	3	9
Feronia cupraea	–	–	–	–	–	–	1	3	6

supports a poorer fauna than cultivated open ground. The rank growth tends to obstruct the floor completely and such litter as is provided by the clumps of briars, brambles and privet remains close to the bushes where it originates and does not become generally spread.

Table 3. *The relationship between diet and distribution, the beetles being grouped into tribes with known dietary requirements*

	Rushy Mead	Mill Copse	Mill Field
Nebriini	131	4	63
Notiophilini	21	1	11
Loricerini	9	–	5
Trechini	8	5	3
Agonini	3	–	2
All carnivores	172	10	84
Bembidiini	35	7	8
Feroniini	46	32	8
All scavengers	81	39	16
Harpalini	1	7	12
Amarini	–	23	6
All herbivores	1	30	18

Not only does the species composition change along the series of traps as arranged in Table 2, but the total number of carabids per trap declines more or less regularly, at least as far as Mill Copse trap C. These changes can best be under-

stood on the basis of diet which varies considerably in the family despite the fact that the carabids are generally thought of as active carnivores. From an examination of the crop contents of eighty-four species of carabids, Davies (1953) has elucidated the diet of many of the adults of the common British species. In Table 3, the beetles captured have been arranged in tribes which show consistent dietary characters, though it must be remembered, as stressed by Davies, that the scavenging groups, especially the Bembidiini, may not be exclusively scavengers. Of the carnivores captured 63% were taken in Rushy Mead and only 4% in Mill Copse whereas for the herbivores the relationship is reversed, 60% being taken in

Table 4. *Summary of the period of capture in the time-sorting pitfalls*

Period 1 runs from midnight to an hour before sunrise, period 2 continues to an hour after sunrise, 3 from then until noon, 4 from noon to an hour before sunset, 5 to an hour after sunset, and 6 from then to midnight.

RM, Rushy Mead; MC, Mill Copse

	Periods											
	1		2		3		4		5		6	
Habitat	RM	MC	RM	MC	RM	MC	RM	MC	RM	MC	RM	MC
Leistus ferrugineus	–	–	–	–	–	–	1	–	–	–	–	–
Nebria brevicollis	30	2	2	–	–	–	–	–	7	1	46	3
Notiophilus substriatus	–	–	–	–	1	–	3	–	1	–	–	–
N. biguttatus	–	–	–	–	4	–	7	–	–	–	–	–
Loricera pilicornis	1	–	–	–	–	–	–	–	–	–	1	1
Asaphidion flavipes	1	–	–	–	2	–	1	–	–	–	–	–
Bembidion quadrimaculatum	–	–	–	–	–	–	–	–	–	–	–	1
B. biguttatum	–	–	–	–	–	–	–	–	–	1	–	–
B. guttula	–	1	–	–	–	–	–	–	–	–	–	–
Trechus secalis	–	–	–	–	–	–	–	–	1	–	–	–
Badister bipustulatus	–	–	–	–	–	–	1	–	–	–	–	–
Harpalus rubripes	–	–	–	–	–	–	–	1	–	–	–	–
Amara communis	–	–	–	–	–	1	–	1	–	–	–	–
A. aenea	–	–	–	–	–	–	–	1	–	–	–	–
A. familiaris	–	–	–	–	–	–	2	1	–	–	–	–
A. plebeja	–	–	–	–	–	–	–	1	–	–	–	–
Feronia cupraea	–	–	–	–	–	2	–	–	–	–	–	–
F. vernalis	–	–	–	–	–	–	1	–	–	–	–	–
F. melanaria	–	–	–	–	–	–	–	–	–	1	–	–
F. madida	4	5	1	–	–	2	–	8	5	1	17	–
Calathus piceus	3	–	–	–	1	–	–	–	3	–	8	–

Mill Copse and only 2% in Rushy Mead. Many of the predatory ground beetles, for example *Notiophilus*, *Leistus*, *Loricera* and to some extent *Nebria*, are specialized predators on Collembola and mites, and these are at their most abundant where there is a rich litter layer undergoing rapid decomposition. Much of the difference between the traps can therefore be related to the prevalence of litter.

The sampling periods into which the 24 h cycle was divided by the time-sorting pitfalls and the numbers of carabids taken are given in Table 4. With the exception of *Nebria brevicollis*, *Notiophilus* and *Feronia madida*, which will be considered below, the numbers are rather small for establishing the limits of the activity periods, but the herbivores are clearly diurnal animals, the single member of the

Harpalini and all of the Amarini being caught during the day time. It has already been shown (Williams 1959) that total activity in Mill Copse is diurnal whereas total activity in Rushy Mead is spread more evenly between night and day, and the problem arises as to how this is effected when a family such as the Carabidae is common to both habitats. In part, the answer would seem to be that the carabid fauna of open terrain such as Mill Copse differs in its species composition from that of woodland and is richer in herbivores, which are diurnal. Other beetles, such as *Feronia cupraea* (L.), which are characteristic of open ground (Larsson 1939) would also seem to be diurnal if the small numbers caught in the pitfalls can be used for such a broad generalization.

NEBRIA BREVICOLLIS

The distribution and life-cycle of *N. brevicollis* is familiar in its general outlines, for both larvae and adults are surface-running forms and are readily caught in pitfalls, unlike many carabids which have subterranean larvae. Pitfalls do not give a true record of the relative numbers of the different larval instars, for the

Table 5. *The distribution of the different stages in the life history of* Nebria brevicollis

	Instar I	Instar II	Instar III	Adult
Rushy Mead	95	83	164	130
Mill Copse	3	1	1	3
Mill Field	24	25	52	63

$\chi^2 = 10{\cdot}57$

earlier stages are obviously not caught in a representative fashion, but, at least, they indicate presence or absence at different times of the year.

N. brevicollis is essentially a woodland species associated with the litter of deciduous trees where the soil moisture is high (Lindroth 1945), and the captures by the simple pitfalls are in accord with this, for the highest numbers were taken in Rushy Mead and Mill Field trap C (Table 1). Its presence in Mill Copse and in the more open parts of Mill Field shows that it is not restricted to woodland, and this departure from the typical habitat has also been noted by Lindroth, and has been given more weight by Burmeister (1939). The adult beetles caught outside Rushy Mead do not represent strays from woodland, for the various stages in the life history are all equally represented, as can be seen from Table 5 in which the different instars are tabulated by habitat. The value of χ^2 is not significant, so there is no evidence to doubt the hypothesis of equal distribution of all stages, and this suggests that breeding occurs in each habitat.

In the terminology of Lindroth (1945), *N. brevicollis* is a larval overwintering species (autumn breeder of Larsson (1939)) but it is atypical in that the callow adults emerge in the spring and then enter a period of diapause before resuming activity in the autumn breeding season (Gilbert 1958). The pupae are found in cells which are rather shallow, being about 1-5 cm below ground (Davies 1955).

As in all the Carabidae (van Emden 1942), there are three larval instars, the first being immediately recognizable by the presence of the 'eggburster' on the head though each instar is readily distinguishable by size as there is no overlap in the ranges of cranial diameter. Table 6 gives the width of the head as measured under the binocular microscope at a magnification of ×70, and the theoretical ranges (mean ±3 standard deviations) show that there would be no confusion of instars separated by this means.

The course of the life history in Rushy Mead is displayed in Fig. 1 in which are plotted the numbers of each instar taken at each collection. The adults are abundant and breeding in September and October, but after that the numbers fall to a low and approximately constant level. It is likely that breeding on a small scale continues throughout the winter as conjectured by Burmeister (1939) and stated by Davies (1955), for the first instar larvae are present continuously, and indeed show a slight increase toward the end of winter. About 2 months after adult activity is at its maximum, the first instars reach their peak, followed a month later by the second instar peak and a further 2 months later by the third

Table 6. *Head widths (mm) of the larval instars of* Nebria brevicollis

Instar	Number measured	Mean	Standard deviation	Calculated range
I	116	0·88	0·04	0·76–1·00
II	91	1·23	0·04	1·11–1·35
III	194	1·74	0·07	1·53–1·95

instar maximum. There would appear, therefore, to be a long breeding season combined with steady development during the winter, so that all stages are present at the same time, as noted by Larsson (1939) in Denmark. The next generation of adults emerges in May and are active before entering diapause, which is presumably associated with the ripening of the gonads, for these are extremely small in the spring adults (Davies 1955).

The relationship between the number emerging in the spring and the number active during the breeding season is a point which merits further research. In Rushy Mead, spring captures were much lower than those in the succeeding autumn, which suggests either that not all the adults emerge in the spring, or that adults are not as active at this time, thus reducing the probability of capture by a technique which depends on the animal's own movement. In November 1952 the trapping area in Rushy Mead was flooded, and this may have led to a high mortality of the larvae, giving very few spring adults, a dearth made good later by immigration. This explanation of the small spring catch may be dismissed since the number of third instars surviving through the winter greatly exceeded the number of adults emerging in spring. Moreover, Rushy Mead is far from any other wooded area which could serve as a rich source of immigrants, and is further isolated by a series of drainage ditches which almost completely surrounds the wood, the only gap being to arable land. A peak in the spring which is smaller than that of the autumn agrees with the findings of Gilbert (1958) who also worked in British

woodland. For Sweden, Lindroth gives a bimodal curve with the spring numbers greater than those of the autumn and this has also been found in Mill Field, as shown in Fig. 2, Mill Field differing from the Swedish condition in the complete absence of activity between the two peaks. A further variation is shown by Larsson's observations in Denmark, where emergence and breeding are combined to give a smooth unimodal curve with a peak in July and August, and with only the slightest indication of a break in May, which may well be due to sampling

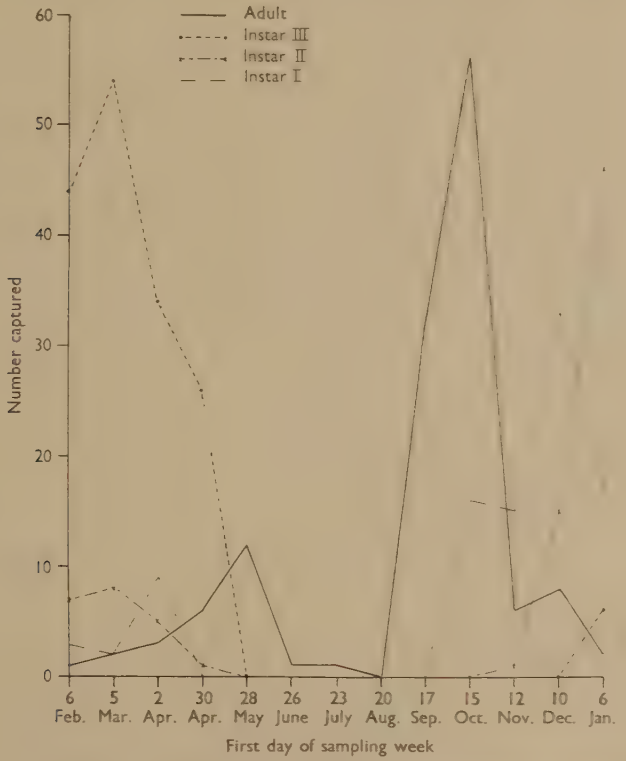

Fig. 1. Captures of the different instars of *Nebria brevicollis* at 4-weekly intervals in pitfalls in Rushy Mead.

error. Comparison of the variations cited suggests that in all instances the adults are emerging from the pupal cell in May, but that some factor then operates to impose a delay in the onset of breeding which is progressively postponed in the order Denmark, Sweden and Britain, and this delay is accompanied by a diapause which becomes more intense the longer breeding is postponed. Whether this series is strictly a geographical one is not clear, for although the continental figures probably are from woodland, this is not certain.

The time-sorting pitfalls show that *Nebria* adults are strictly nocturnal (Table

4). The periods given in Table 4 are not of equal duration, so in Table 7 the numbers of adults caught are recalculated to the number which would be caught if each period were of 100 h duration. For comparison, the quadrat counts have been grouped into the same periods and adjusted to periods of 100 h. No adults were taken during the hours of daylight by either sampling method, and the broad groupings imposed by the rotary trap technique suggest that activity starts about sunset and continues through the night, but is predominantly before mid-

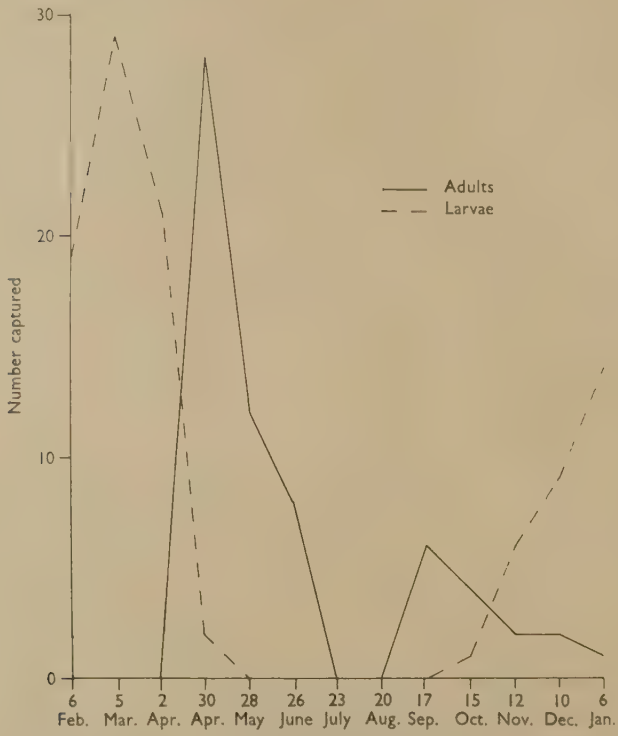

Fig. 2. Captures of *Nebria brevicollis* adults and larvae at 4-weekly intervals in pitfalls in Mill Field.

night. The narrower time intervals of the quadrat counts allow this point to be tested more stringently as the time of capture is known. Thus, if the captures of adult *Nebria* in September, when they were more abundant, are grouped in 2 h periods, starting at sunset, four were taken in the first period, five in the second, two in the third, and one each in the fourth, fifth and sixth periods, midnight coming between the third and fourth. In this single instance, a rapid onset of activity with sunset and a decline during the later hours of darkness is clearly shown.

Larval *Nebria* are also nocturnal, in general, as shown by the numbers caught in

the pitfall in Rushy Mead (Table 8), but their nocturnal habit is not as rigid as that of the imago, a few being caught during daylight and the remainder being caught more uniformly during the hours of darkness. There is some evidence that

Table 7. *The numbers of adult* Nebria brevicollis *caught during different periods in pitfalls and quadrats*

The limits of the periods are given in Table 4

		Periods					
		1	2	3	4	5	6
Caught in pitfalls		32	2	–	–	8	49
Caught in quadrats		5	–	–	–	4	9
Hours per period	pitfalls	82	32	78	79	32	81
	quadrats	8	4	12	12	4	8
Adults per 100 h	pitfalls	44	6	–	–	25	61
	quadrats	62	–	–	–	100	112

the sharply restricted activity period of the adult is developed during the individual life-cycle, though the number of first instars taken in pitfalls is rather small. By amalgamating the records of first and second instars to give the behaviour of the early stages, and by combining periods 1, 2 and 6 to give a nocturnal fauna as

Table 8. *The numbers of larval* Nebria *caught in the Rushy Mead pitfall at different periods*

The limits of the periods are given in Table 4

	Periods					
	1	2	3	4	5	6
Number of larvae	24	8	2	5	3	22
Number of hours	50·5	18	39·5	40	18	50
Larvae per 100 h	48	45	5	12	17	44

opposed to the diurnal fauna of periods 2, 3 and 4 (Williams 1959) some comparison can be made, as in Table 9. The last larval instar has acquired the same pattern of activity as the adult, but the younger larvae spread their activity uniformly.

Table 9. *The nocturnal and diurnal activity of adult* Nebria *compared with early instars and the last larval instar*

Periods	Nocturnal 1+2+6	Diurnal 3+4+5	% Nocturnal –
Instars I and II	5	5	50
Instar III	49	5	91
Adult	83	8	91

NOTIOPHILUS

Pitfall traps do not give a very representative sample of *Notiophilus*, for close observation at Rushy Mead, where the genus is abundant, showed that the beetles were able to avoid the traps and were not caught at random. Pitfall counts,

therefore, do not give a true indication of the abundance of these beetles and interpretation of the results must be made with some reserve. The captures are in agreement with those of Larsson (1939) and Lindroth (1945); *N. palustris* being confined to grassland, *N. biguttatus* to woodland and *N. substriatus* and *N. rufipes* being similar to *Nebria brevicollis*, *i.e.* predominantly but not exclusively woodland species. All the species represented in the present study are recorded as spring breeders and may be considered together. Table 10 displays the numbers of adult

Table 10. *The numbers of* Notiophilus *and* Feronia madida *adults taken in simple pitfalls*

	Sampling week beginning												
	6 Feb.	3 Mar.	2 April	30 April	28 May	26 June	23 July	20 Aug.	17 Sept.	15 Oct.	12 Nov.	10 Dec.	6 Jan.
Notiophilus	0	1	1	15	9	4	0	0	1	1	0	1	0
Feronia madida	0	0	1	2	6	3	13	7	6	1	0	0	0

Notiophilus caught through the year, the larvae being taken in small numbers in April, May and June. The adults emerge from hibernation early in the year and are at their maximum in May and June. These are the breeding adults and are followed by the larvae which give rise to the second generation of adults which are active without breeding during the autumn and early winter until they go into hibernation for the most severe part of the winter.

The diel periodicity of *Notiophilus* adults and larvae, as shown by pitfall and

Table 11. *The number of adult and larval* Notiophilus *taken in the pitfall and the quadrats in Rushy Mead during the different periods*

		Periods					
		1	2	3	4	5	6
Adults in pitfall		–	–	5	10	1	–
Adults in quadrats	Sept.	–	1	5	3	1	1
	May	–	–	5	5	–	1
Larvae in pitfall		–	–	–	10	–	–
Adults per 100 h	pitfall	–	–	9	18	6	–
	quadrat, Sept.	–	50	100	60	50	20
	quadrat, May	–	–	72	72	–	33

quadrat captures, is given in Table 11. In the pitfalls, *Notiophilus* was caught only during daylight, and this diurnalism applies to both larvae and adults. Some adults were taken during darkness in the quadrats, but it is probable that these were stimulated into movement by the light by which the quadrat was examined. The pitfalls would be expected to catch *Notiophilus* more efficiently in the dark than in the light, for vision is the most important sense in this genus, as is shown by the well-developed eyes. Absence of beetles from the pitfalls at night is more reliable evidence than their presence in the quadrats.

FERONIA MADIDA

Little is known of the life history of *F. madida*, which is surprising as it is one of the most ubiquitous of the carabids. The adults are readily caught in pitfalls but the larvae are subterranean and only occasional captures are made. The adults are active throughout a great deal of the year as can be seen from Table 10 which summarizes the results of the simple pitfalls. Burmeister (1939) states that copulation takes place in spring and autumn; adults maintained in the laboratory for experimental purposes readily copulated in August, September and October but showed little inclination to do so at other times of the year.

The diel captures of this species are given in Table 4 and provide an interesting contrast to the other species considered. In Rushy Mead, *F. madida* was active only at night, a pattern similar to that of *Nebria*, whereas in Mill Copse most of the individuals were caught during the day. Thus the periodicity of *Feronia madida* depends on the habitat in which it is taken, and this parallels the findings of Krumbiegel (1932) who found for *Carabus nemoralis* Müll. that in Europe the northern and eastern forms are nocturnal while the southern forms are diurnal. This rather paradoxical result for *Feronia madida* is consistent with the general impression that one gets from the many occasions when this species is encountered. Generally, it is to be found during the day under stones, etc., often in a rigid state of catalepsis which shows that it has not simply come to rest to escape observation. Country householders often find it in the house in large numbers in the morning, having been trapped indoors during its nocturnal wanderings, and this has been reported to me on a number of occasions by people who fear that they have suffered an invasion of cockroaches, for *F. madida* is most convincingly a 'black beetle'. Despite a large number of such casual observations which reinforce the impression of its nocturnalism it is sometimes seen on the brightest of days moving under conditions which preclude the possibility of its disturbance by the observer, and such diurnal movement is always in open, grassy localities.

This type of activity does not concur with the general condition of a short and fixed activity period during the 24 h cycle and was therefore investigated experimentally. The periods adopted in the time-sorting sampling were more nearly related to light intensity than to any other single physical factor, periods one and six being dark, periods three and four light and periods two and five transitional. Changes in temperature and humidity are not in phase with changes in light intensity owing to the lag in warming and cooling following sunrise and sunset. In addition, the individual periods are so long that physical conditions, other than light, were very different at the beginning and end of a period. As the difference in periodicity was demonstrated by the rotary pitfalls, it was decided to restrict the experimental investigation to the effect of light on activity; but as some sort of feeding regime had to be imposed on the beetles in the laboratory the effect of hunger was also included.

The beetles were tested individually in actographs, of which two types were used. The simplest consisted of a tilting arena which made an electrical contact as it was depressed and was thus made to record on a smoked barograph drum. The arena

was a circular Perspex dish 15 cm in diameter, with walls 1·5 cm high supporting an overhanging flange 1·5 cm wide. This dish was balanced in a transverse axis by a pair of gramophone needles which were received into jewel bearings taken from discarded moving coil instruments. The horizontal flange was effective in preventing escape when the beetles were confined for only a short time, but occasionally during longer experiments a beetle would be successful in climbing out, and to prevent this a perforated collar was fitted against the flange to make a closed channel around the periphery of the dish. The arena was enclosed in a large transparent chamber containing dishes of water to maintain a saturated atmosphere, and the tank was kept in a cellar which was constantly at a temperature of 18° C during the experiments. Light was provided when required by a 25 W bulb

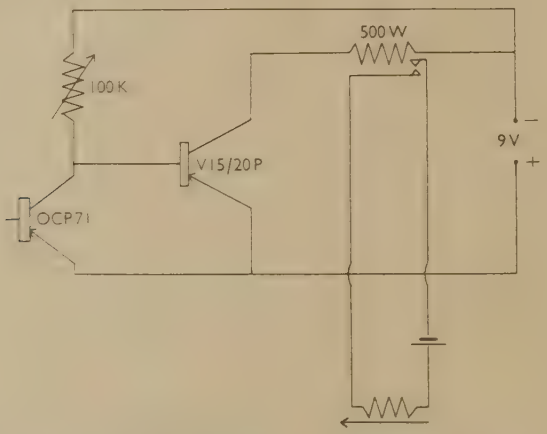

Fig. 3. Circuit diagram for the infra-red actograph. The source of light is not shown but is focused on to the photo-transistor OCP 71 and traverses the channel within which the beetle is confined.

suspended 2 ft above the arena and outside the tank, with a dish of water below it as a heat filter.

The alternative type of actograph recorded the number of times a beetle interrupted an infra-red beam. The beetle was confined to a circular runway across which was projected a beam of light, focused on a photo-transistor (Mullard OCP 71). Current changes in the photo-transistor, caused by the passage of the beetle, were amplified by a power transistor (Pye V15 20P) and operated a relay writing on a smoked barograph drum. The wiring diagram of this apparatus is given in Fig. 3. A deep red filter was used to give infra-red and red light, the red beam being visible to the experimenter for monitoring.

For the first experiments, two female *F. madida* from Rushy Mead were used. They were maintained under normal fluctuating conditions in the laboratory and provided with ample food consisting of decapitated mealworms, which they ate readily. They were used alternately in an actograph for periods of 24 h, the

treatment given during each period being determined at random from the four possibles: 24 h continuous light, 24 h continuous darkness, 12 h light followed by 12 h dark, or 12 h dark followed by 12 h light. Successive experiments were started at different times to ensure that experimental and GMT did not bear a constant relation to each other, and were continued until each beetle had been subject to each treatment three times. The resulting distribution of activity is shown in Fig. 4. Where light and darkness are given during the same period, movement is predominantly in the dark phase; where uniform conditions are held for the 24 h, the amount of movement in continuous light is much less than that in continuous darkness. For the complete series of twenty-four experiments, 84% of the recorded movement was in darkness, a not unexpected result for a nocturnal species. The

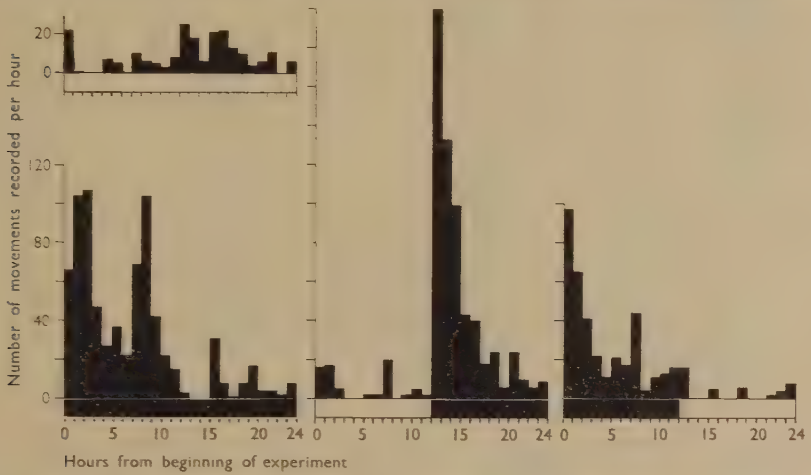

Fig. 4. Activity of *Feronia madida* during 24 h of constant or alternating light and darkness. Each histogram is the sum of 6 separate days, and the movements recorded are the displacements of a tilting arena. The light conditions are indicated by a horizontal bar, black for darkness and white for light.

relationship between light conditions and movement is not a simple one, for the complementary experiments in which light and darkness are included in the same period do not give results which are mirror-images of each other. Activity is greatest when darkness follows a period of light. Even in continuous light, some movement does take place and tends to increase towards the end of the period, while in continuous darkness there is a decline in activity. A simple mechanism such as: illumination, no activity; darkness, activity, is therefore not sufficient explanation, for the response of the beetle alters with time, suggesting that other factors such as rhythmic processes, hunger or fatigue are at work.

Examination of the individual traces from a number of experiments shows that there is a short-term rhythm of activity with a period of about 4 h. During times of comparative inactivity single movements are made at this frequency, as are the bursts of movement during active periods. To detect rhythms of longer period,

individual beetles were maintained in actographs under uniform conditions until they died or until they became too sluggish to move. Under such conditions, all beetles showed a marked intrinsic rhythm of approximately 24 h. Under such uniform conditions, the amount of activity falls off sharply, so the longest term results have been selected for display in Fig. 5. Here the individual days are shown for a single beetle in constant darkness, and the days in groups of three

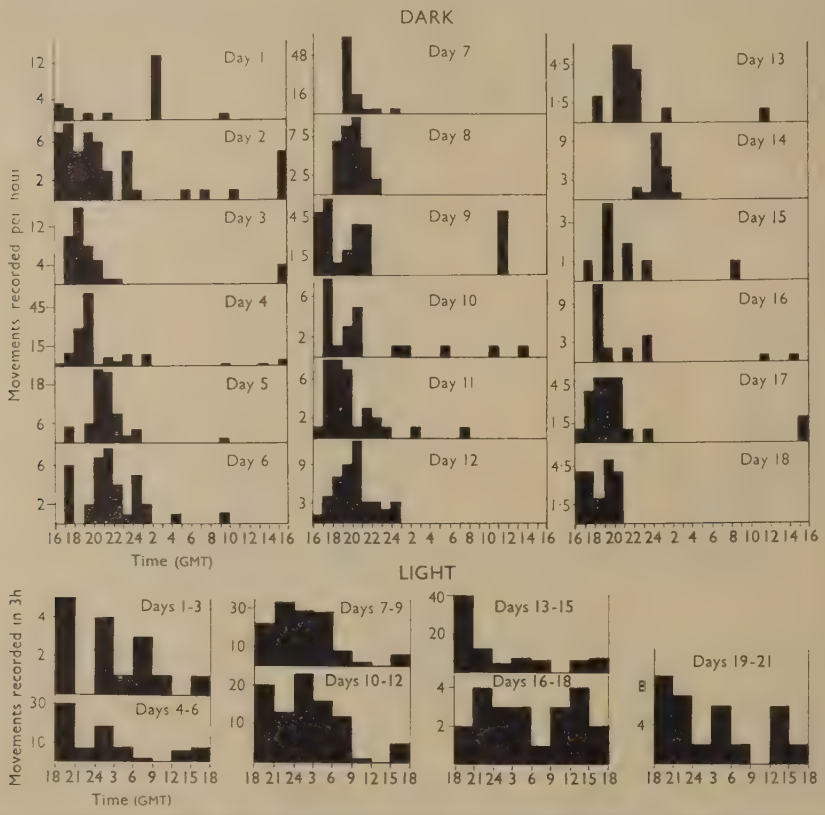

Fig. 5. Activity of *Feronia madida* during 18 days in constant darkness and 21 days in constant light. The recorded movements in light are summed over 3 h periods, and the days are also summed in threes.

for a beetle in constant light, with a time unit of 3 h as activity is low. In the dark, time-keeping is quite good and maintained throughout the experiment, while in the light the efficiency of time-keeping is not so good and varies through the experiment, being better at the beginning and the end and falling off in the middle.

The effect of hunger on the response to light was determined by trapping a beetle in Rushy Mead and keeping it for 5 days in the pitfall from which other organisms were excluded by a wire mesh. It was then placed in an actograph and

its movement recorded in continuous light. The result is shown in Fig. 6. The activity of this beetle in light is at the same level as that of well-fed beetles in the dark, and is continuous, showing that hunger overcomes the inhibition by light. To check that the beetle was in fact hungry, it was fed to repletion at the end of the experiment, when it consumed three mealworms. This compares with the half mealworm taken at the end of a day by the others.

There are, therefore, at least three factors which determine the time of activity of *F. maidida* adults: an intrinsic 24 h rhythm, inhibition of movement by light, and removal of this inhibition by hunger. The interaction of these factors has been investigated in further experiments. These are similar in plan: a beetle is kept in the actograph until its intrinsic rhythm is obvious, and then light condi-

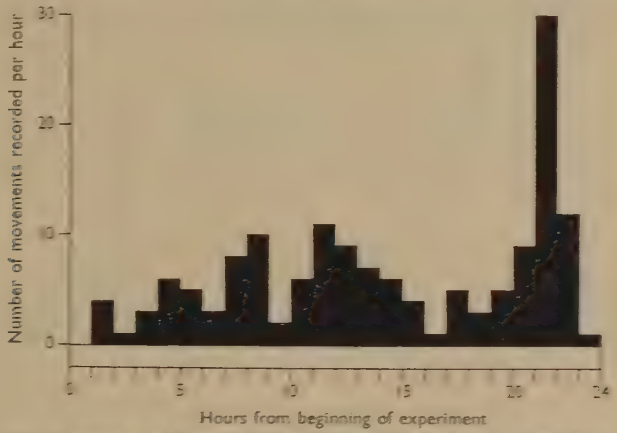

Fig. 6. Activity of *Farsima maidida* in constant light after withholding food for 5 days.

tions or feeding times are manipulated to induce movement in the inactive phase and, if possible, to eliminate the appearance of the intrinsic rhythm. When a new periodicity has been established, uniform conditions are reimposed and the activity pattern is recorded until the beetle's death. The greatest difficulty encountered in this type of experiment was the decline in activity under constant conditions, a decline which disappears when the beetle is returned to the normal room fluctuations. Thus, if several days are allowed to elapse so that the intrinsic rhythm shall be clearly displayed, then the beetle becomes inert when attempts are made to condition it by light or feeding. The most complete record for the interaction of light and intrinsic rhythm is shown in Fig. 7. Having found that each individual has an intrinsic rhythm which is quickly displayed in constant conditions, the beetle figured was left for only 1 day in continuous darkness. It was then subjected to alternating light and dark for 3 days, the light phase spanning the original time of activity and food being given at the beginning of the new dark phase to reinforce the shift occasioned by light. After 2 days of such treatment, activity had been moved completely out of phase with the original rhythm.

On return to continuous darkness, the induced periodicity persists for a time, though waning, while the intrinsic rhythm is re-established. There is some indication of the return of the rhythm on the third day in the light, but this may

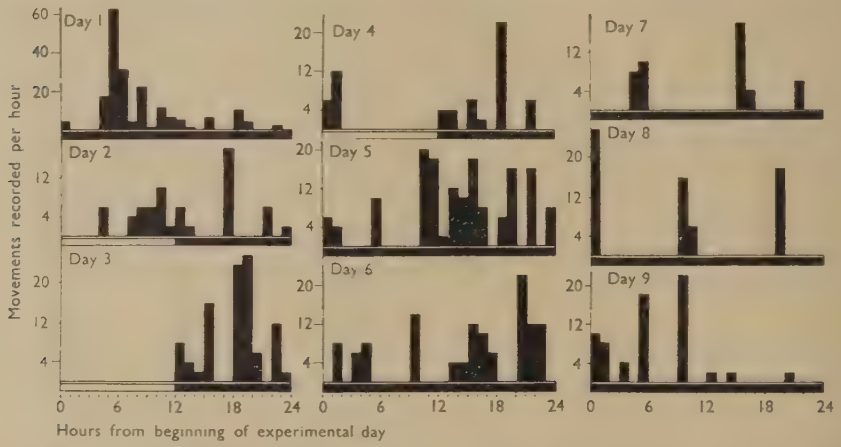

Fig. 7. The interaction between the intrinsic activity rhythm of *Feronia madida* and light. The light conditions are indicated by a horizontal bar, black for darkness and white for light.

be a response to the sudden light stimulus as it is a transient burst of movement. To determine whether the rhythm is re-established against the inhibition of movement by light, a similar experiment was performed without the eventual return to constant darkness. This is illustrated in Fig. 8, where the first histogram is the

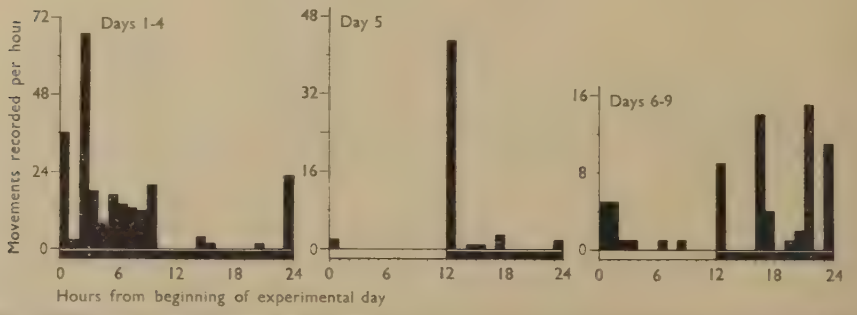

Fig. 8. The interaction between the intrinsic activity rhythm of *Feronia madida* and light. The light conditions are indicated by a horizontal bar, black for darkness and white for light.

sum of activity through 4 days in constant darkness and indicates a pronounced rhythm. The second histogram is of the fifth day when light was introduced, with the complete suppression of the rhythmic activity and a shift of movement to the dark phase. The third histogram is the sum of movement during the remaining 4 days of alternate light and dark; it can be seen that activity is resumed at the time

of the intrinsic activity, and extends over more hours than movement which is simply a response to the switching on of the light.

The effect of feeding on periodicity is illustrated in Fig. 9. A *F. madida* adult was kept for 2 days in darkness without being fed, and the hourly disposition of movement is given in the first histogram. There was little activity for the first 5 h so for the succeeding 4 days food was presented during this inactive phase and left in the actograph for 6 h (second histogram). The presence of food stimulates the beetle to search so that the feeding period is associated with movement, and the beetle begins to move in anticipation of the feeding time as is shown by movement during the last hour of the experimental cycle. When food is withheld on the last day (third histogram), there is no movement, nor does the beetle move during the last hour in anticipation of food on the following day. Periodicity of movement which has been induced by a regular feeding time may be maintained against the

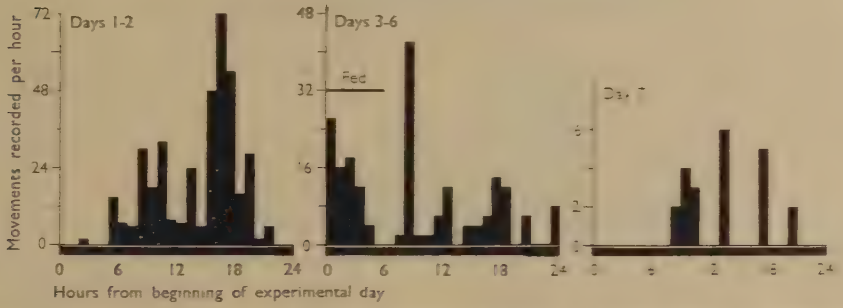

Fig. 9. The effect of regular feeding on the periodicity of a mutant of *F. madida* in continuous darkness.

inhibitory effect of light, as shown in Fig. 10. A beetle left for 3 days in continuous darkness (first histogram) demonstrates a rhythm and periodicity is then induced by feeding for 3 days during the last 6 h of each experimental day (second histogram). For the final 3 days (third histogram) light is given during the last 12 h of each day, but the feeding regime continued, with the result that the beetle remains active at the time of feeding although movement is now in the light.

The experiments which have been selected for demonstration are those in which the beetles remained active for a sufficiently long time for the completion of the experiments. Most of the replications ended before yielding all the required information, as the beetles became inert. Use was made of these replications to vary the number of days of the conditioning stimuli. So far as they go, they serve to confirm the isolated complete results and the following generalizations may be made. All adult *F. madida* show an intrinsic rhythm of activity with peaks at intervals of approximately 24 h. The overt demonstration of this rhythm may be suppressed by giving light at the time of normal activity and movement shifted to any part of the 24 h cycle by a complementary dark period. On return to constant darkness, the intrinsic activity pattern re-emerges, and it re-emerges though

more slowly, even against the inhibitory effect of light. Periodicity may also be induced by feeding out of phase with the intrinsic activity, and such a periodicity can also be maintained against inhibition of movement by light if the feeding stimulus is regularly maintained.

Although light and feeding times may be manipulated to give a periodicity of locomotor activity, this is not maintained if the imposed stimulus is removed and

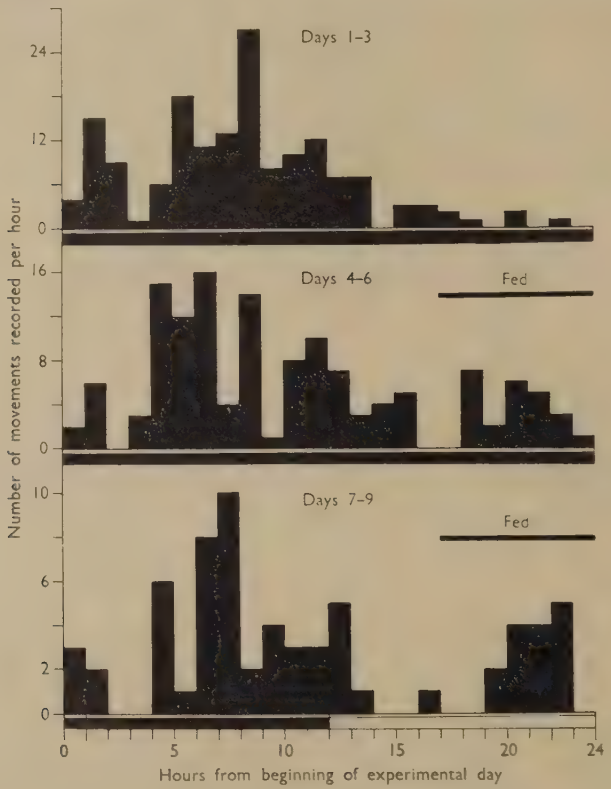

Fig. 10. The effect of regular feeding on the periodicity of activity of *Feronia madida*. Light conditions are indicated by a horizontal bar, black for darkness and white for light.

in no experiment has it been possible to establish a true rhythm which persists under uniform conditions. No explanation can be given, therefore, of the way in which the original diurnal rhythm is established in the field, whether, for example, it is genetically determined or established once and for all in early adult life. It has not yet been possible to rear the animals in the laboratory and recourse has to be made to individuals taken from the field, and these are of unknown age. Adult *F. madida* taken in the early spring, when they are probably newly emerged, do not give such clear patterns of activity as those taken in the autumn, which

suggests that the rhythm is acquired during adult life, but they do not show much activity at all in the actograph so it is difficult to assert that a rhythm is or is not present.

The experiments described above were made with beetles taken from Rushy Mead, or taken during the day in convenient gardens and found hiding under debris. The final experiments were performed with beetles from Mill Copse to see how these differed from those from Rushy Mead. Altogether about twenty beetles from Mill Copse and Rushy Mead have been used to determine the time of the peak of their intrinsic rhythm when placed in continuous darkness. *F. madida* adults from Rushy Mead show active periods with their modal points during the night, varying between 1800 h GMT and 0200 h GMT. The spread of the times of the natural rhythm of Mill Copse beetles is wider, being from 1700 to 0800 h GMT, but not one of these can be claimed as markedly diurnal, for rhythms furthest from midnight are shown by beetles taken from October onward when the night is much longer. The intrinsic activity rhythm of all *F. madida* tested has therefore been a nocturnal one regardless of the habitat from which they were taken. The Mill Copse beetles differed from those from Rushy Mead in that the true intrinsic rhythm was not displayed until a day or two of constant conditions had elapsed, during which time movement during daylight hours decreased and threw into relief the nocturnal rhythm. A further difference was the response to alternate light and dark. The Rushy Mead response has been shown in Fig. 4 where light inhibits movement; twelve Mill Copse beetles taken fresh from the field and placed in actographs for a day under a regime of 12 h light and 12 h darkness gave a total of 6129 movements of the tilting arena, of which 3231 (53%) were made in the light.

An attempt may now be made to explain the diurnal activity of *F. madida* in Mill Copse and its nocturnal activity in Rushy Mead. The species is not restricted to a particular habitat and appears to be wide-ranging, so that a single adult would pass freely from open to woodland areas and vice versa. A newly emerged adult would show a marked nocturnal rhythm of activity, and in woodland with a rich nocturnal fauna (Williams 1959), its movement would lead to the capture of food, assuming that it was living on moving prey. Thus its own rhythm would be reinforced by successful capture of food and it would remain strictly nocturnal. In open country there is little nocturnal activity (Williams 1959), so that the intrinsic nocturnalism of a *F. madida* adult would not lead to successful feeding. For the hungry individual light is not inhibiting, and its short-term rhythm would ensure that some movement was made during the day. If this led to food capture, then a periodicity would be established, and the beetle would become diurnally active for as long as it succeeded in obtaining food at this time. The intrinsic nocturnal rhythm would not be suppressed and it would continue to move at night. In this way, the predominantly diurnal catch, with some nocturnal captures, which has been found in Mill Copse, would be explained. If the beetle wandered back into woodland it would feed successfully during its rhythmic phase of activity and its diurnalism would again fade.

The main objection to this thesis is that it assumes that *F. madida* is dependent upon living prey which is taken while the prey is moving. Davies (1953) decided that *F. madida* was a scavenger and its success in a variety of habitats was due to the wide range of food which it would accept. Examination of crop contents, the method employed by Davies to determine the diet, does not give any indication of the state of the food at the time of capture, so it may well be that this species is a generalized carnivore rather than a scavenger. In the laboratory it will eat a variety of dead foods but this is also true of such carnivores as *Nebria brevicollis* so that these artificial conditions cannot be taken as reliable indications of food in nature.

DISCUSSION

From the very large number of observations that have been made (Calhoun 1944-6, Harker 1958), it is clear that few animals are continuously active or completely arhythmic with respect to the 24 h cycle of day and night. A period of activity is normally followed by a period of rest and if a number of species co-exist with activity periods which are not in phase, then a 'shift system' will seem to be operating. To some extent such an orderly succession of activity peaks may be accidental, but when two or more species are dependent upon the same food supply, it is often assumed that phased activity represents a method of avoiding competition. Such an interpretation of the obvious distinction between the nocturnal fauna and the diurnal fauna of a community seems to be well established in ecological thought, and is given prominence in elementary text books on ecology (*e.g.* Sankey 1958). Such shift systems do occur, if competition can be assumed, as is seen in the relationship between *Nebria brevicollis* and *Notiophilus*. These are the most abundant of the larger arthropod carnivores which forage on the floor of Rushy Mead; their food requirements are much the same, both feeding on the mites and springtails which are present in the litter. From such a conjunction one presumes that they are in competition for food, though it may well be that the population of each is limited by some other factors altogether. If they are competing, the available food supply is utilized more efficiently by the fact that they do not forage at the same time in the same place. The larvae of *Notiophilus* are present during the summer and the larvae of *Nebria* during the winter, giving a seasonal displacement of competitors which may be regarded as an extension of the shift system which is normally thought of in its diurnal sense. The more usual Box and Cox replacement is exemplified by the adults. Although *Notiophilus* is a spring breeder and *Nebria* an autumn breeder, they both have peaks of activity in the spring and autumn, for the breeding season of the one coincides with the seasonal emergence of the other. But they do not meet in direct competition for the capture of a particular springtail, for *Notiophilus* is strictly diurnal and *Nebria* strictly nocturnal.

When the number of such associations is multiplied, it is natural to think of a shift system as an essential part of the dynamic structure of the community. However, Park (1941) has suggested that activity which is disposed symmetrically

around the 24 h cycle is characteristic only of an evolved community and that activity in a primitive community will be markedly asymmetrical, with a preponderance during either the day or the night. Williams (1959) studied the locomotor activity of the floor faunas of two contrasted habitats, Rushy Mead and Mill Copse, and showed that the richer fauna (Rushy Mead) displayed symmetrical activity, while the poorer fauna was active for only a part of the day and night cycle, being preponderantly diurnal and thus asymmetrical. Where activity is restricted to a part only of 24 h, it is impossible to talk of a shift system, for all the animals are active at one and the same time. It is interesting to note that this asymmetry is associated with a poorer fauna and so, to some extent, parallels Park's original suggestion.

Such contrasted habitats as Rushy Mead and Mill Copse nevertheless support animals which are included in the same wider taxonomic groupings such as the family and, indeed, have many species in common. By what differences of representatives or behaviour do the animals of such wider groupings contribute to the type of symmetry which is characteristic of different habitats? Taking the Carabidae as an example, the first obvious difference between Rushy Mead and Mill Copse is in the specific composition of the fauna. It is of course by such differences that any case can be made for the existence of a community as such. Rushy Mead provides a rich litter layer, the turnover of which furnishes food for a vast assemblage of cryptozoa which, in turn, provides food for the carnivorous ground beetles. Many of these are absent or only sparsely represented in Mill Copse where the litter layer is virtually absent. In place of the carnivorous ground beetles, most of the comparable predation on the floor of Mill Copse is by the wolf spiders which are poorly represented in Rushy Mead. The carabids of Mill Copse are those species which are either scavengers or herbivores. This distinction alone will account for much of the disparity between the distribution of activity in the two habitats, for some of the carnivores are diurnal and some nocturnal, thus contributing to symmetry in the wood, whereas the herbivores are diurnal and thus emphasize the characteristic asymmetry of Mill Copse. The scavengers which are characteristic of open ground, such as *Feronia cupraea*, are likewise markedly diurnal.

Some species are common to both habitats and would therefore be expected to obscure the clear-cut distinction between the two. If the two breeding stocks were isolated, then each could conform to the type of symmetry characteristic of each habitat in the same way as distinct species. No such case has yet come to light in the present investigation, but a beetle which is abundant in both areas is *Feronia madida*. This has an inherent nocturnal rhythm and is strictly nocturnal in its habit in Rushy Mead. It would be expected that such a species would help to swell the nocturnally active fauna of Mill Copse, but in fact it is predominantly diurnal in that habitat. This accommodation has been shown to be due to the modifiability of its periodicity, hunger removing the inhibition of movement by light, and cyclical feeding maintaining a new periodicity. Such a periodicity is transient and is not carried over with a change back to woodland. The Carabidae,

therefore, although common to both Rushy Mead and Mill Copse, contribute to the symmetry characteristic of each habitat partly by a change in specific composition and partly by a change in behaviour of a species which is found in both.

ACKNOWLEDGMENTS

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SUMMARY

1. The carabid fauna of woodland is more abundant and more varied than that of open country, and this is associated with the litter layer characteristic of woods.

2. Open ground has fewer carnivorous and more herbivorous ground beetles than woodland, and the herbivores are strongly diurnal.

3. *Nebria brevicollis* is an autumn breeder and is strictly nocturnal as late larva and adult.

4. The common species of *Notiophilus* in woodland are all spring breeders and are diurnal as larvae and adults.

5. *Feronia madida* is nocturnal in woodland and mainly diurnal in open grassland. Experimental investigation shows it to have an intrinsic 24 h rhythm with its active phase at night, but the time of movement can be controlled by manipulating the periodicity of feeding and of light. Periodicity which has been induced in this way rapidly fades in continuous darkness.

6. The bearing of these findings on the balance of nocturnal and diurnal activity in different habitats is discussed.

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THE ECOLOGY OF LOUGH INE*
VIII. MUSSELS AND THEIR PREDATORS

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(With 4 Figures in the Text)

Mussels are found in two quite different kinds of habitat between tide marks: open coast, and very sheltered places such as harbours and estuaries. This is true also of the Lough Ine area (Ebling, Kitching, Sleigh & Sloane, in press). Here the open sea *Mytilus* are all rather small, whereas those in shelter at the north end of the lough and in the Goleen include many large ones. *Mytilus* is present both in the straight (*M. edulis*) and hooked (*M. galloprovincialis*) forms (Hepper 1957) and both are present in both types of habitat (Ebling *et al.*, in press). We have also seen *Mytilus* in a third kind of habitat at Lough Ine, sublittorally in strong current on the Sill.

It is possible that the discontinuous distribution of *Mytilus* in the Lough Ine area is due to predation. On this hypothesis the predators would be affected adversely by wave action, by strong current, and also by some condition (possibly low salinity) operating in those parts of the lough least affected by tidal exchange. *Mytilus* would also benefit by situations where it was less accessible, such as deep crevices and vertical rock faces.

The predacious gastropod *Nucella lapillus*† is abundant on the dense beds of small *Mytilus* at open sea stations and is also found on sublittoral *Mytilus* on the Sill. Other possible predators of established mussels include the crabs *Cancer pagurus*, *Xantho incisus*, *Carcinus maenas* and *Portunus puber*, and the starfishes *Asterias rubens*, *Marthasterias glacialis* and *Asterina gibbosa*, all common in the lough. The sea urchin *Paracentrotus lividus* is abundant in the lough, and *Echinus esculentus* is not infrequent from the Bullock Narrows to the south-east corner of the lough. Of these *Echinus* is known to include animal material in its diet. Many other predators may affect the younger stages, so that the problem is likely to be complicated. We have so far confined our attention to *Mytilus* of the range of sizes found at Carrigathorna on the open coast (up to 25 mm in length) and at the north end of the lough (mainly 30-70 mm). Preliminary samples suggest that the small *Mytilus* found at Carrigathorna are almost entirely *M. edulis* and the large ones at the north end of the lough mainly *M. galloprovincialis*, but further investigations will be needed before we can report definitely on the distribution of these two forms or comment on their validity as species.

* Continuing the series 'The ecology of the Lough Ine Rapids with special reference to water currents'.

† All scientific names used in the paper are as in the *Plymouth Marine Fauna* (Marine Biological Association, 1957).

THE SURVIVAL OF *MYTILUS*

Experiments were carried out to test the ability of *Mytilus* to survive at various levels (from the upper littoral to the shallow sublittoral) in various parts of the Lough Ine area. The positions of the various stations are shown in Fig. 1. At all except Glannafeen Beach the shore is of solid rock, sloping moderately or steeply. Glannafeen Beach, chosen for comparison with the nearby Glannafeen Quay, is a gentle slope of small stones and boulders. Small mussels from Carrigathorna were used for the first series of experiments, and mussels, mainly large, from the north end of the lough for the second.

(*a*) *Methods*

Pieces of rock with *Mytilus* attached were removed from the shore with hammer and chisel, stored for about 24 h in an open crate in the shallow sublittoral near Glannafeen Beach, and cemented with a quick-setting mixture of cement, sand

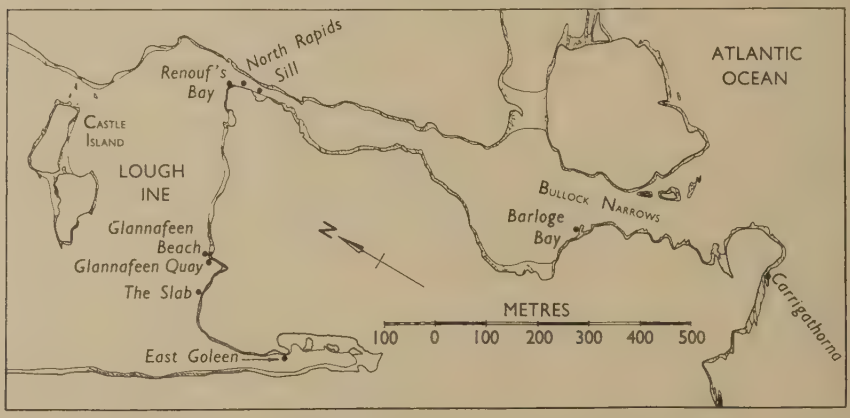

Fig. 1. Map of the Lough Ine area showing the stations used in this work.

and waterproofing compound into their new positions. For sublittoral tests, and also at all levels on Glannafeen Beach, the piece of rock with *Mytilus* was cemented on to another larger rock, and this was placed in the required position after an interval of not more than 12 h for setting, during which the mussels were kept in the shade. No mussels showed any ill effects which could be attributed to transference or cementing. The procedure used for placing *Mytilus* at Carrigathorna had to be modified slightly because of the severe wave action to which this station is exposed. Pieces of rock with *Mytilus* from Carrigathorna were stored for 24 h near Glannafeen Beach and then cemented to the top of a 50 kg concrete block already made at Carrigathorna. After 24 h for setting, the block was placed in a shallow rock pool with the top exposed to air, in the upper part of the *Mytilus* zone. In view of the difficulties at this station, we did not attempt to work at more than one level on the shore. The results support the conclusion that no significant damage was caused to the *Mytilus* by the procedure of transfer.

(b) Results and conclusions

Although up to ten groups of *Mytilus* were affixed at each of the chosen stations, for convenience in presentation the data for each station have been grouped by levels, as indicated by the algal zone. The results are shown in Figs. 2 and 3.

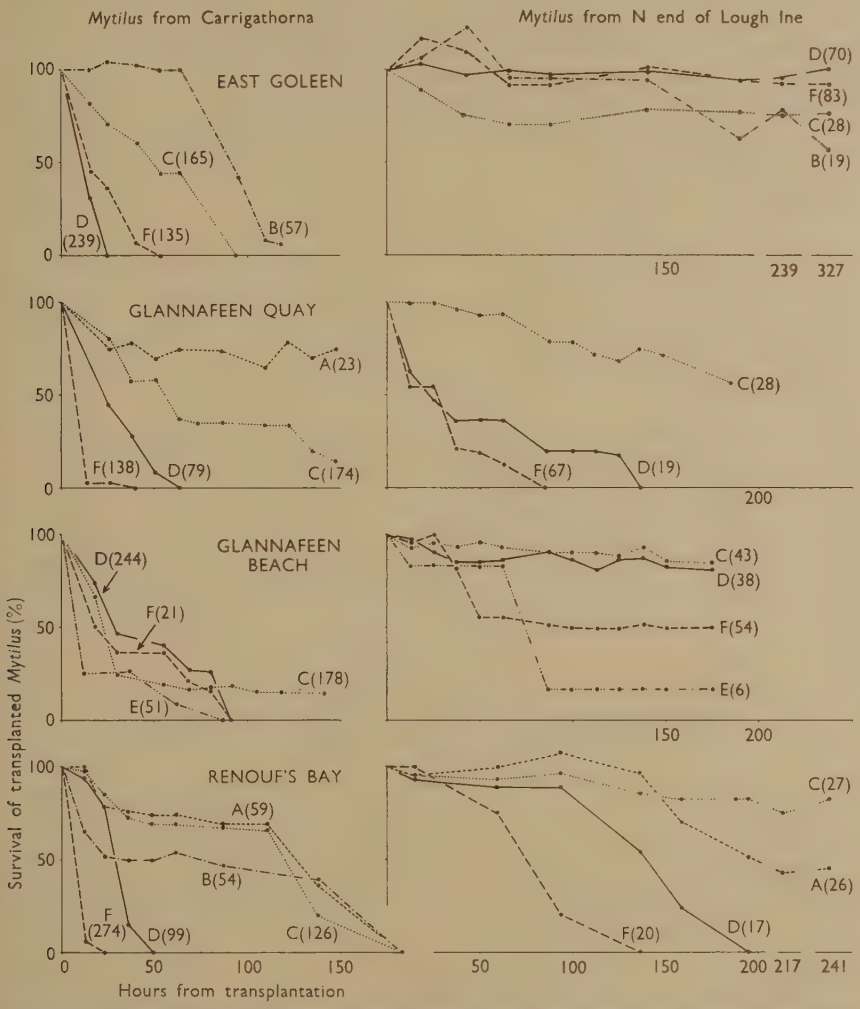

Fig. 2. Percentage survival of mussels from Carrigathorna (small) and from the north end of the lough (large), transferred (with rock substratum) to positions in the lough. The levels of the new positions are indicated by the algal zones as follows: A, *Pelvetia*; B, *Fucus spiralis*; C, upper *Ascophyllum*; D, lower *Ascophyllum* and *Fucus vesiculosus*; E, *F. serratus*; F, shallow sublittoral. The numbers of mussels transferred are given in parentheses.

Small mussels disappeared quickly from all stations except on the open coast at Carrigathorna. Except at the highest levels, they all remained alive and appeared

healthy up to the time of their disappearance. Undoubtedly they fell victim to predators. In general those higher up survived longer, probably because the predators were mainly or entirely marine. Mussels placed in the *Pelvetia* zone died, gaped and eventually were broken up, probably by terrestrial scavengers, possibly birds. This effect was no doubt accentuated in the first series of experiments with *Mytilus* from Carrigathorna because these took place over a period of neap tides, during which the *Pelvetia* zone remains uncovered for several days.

The mussels replaced at Carrigathorna survived much better than those transferred from there to other stations. Although there were a few losses, most of the *Mytilus* remained in position and appeared normal. Unfortunately bad weather

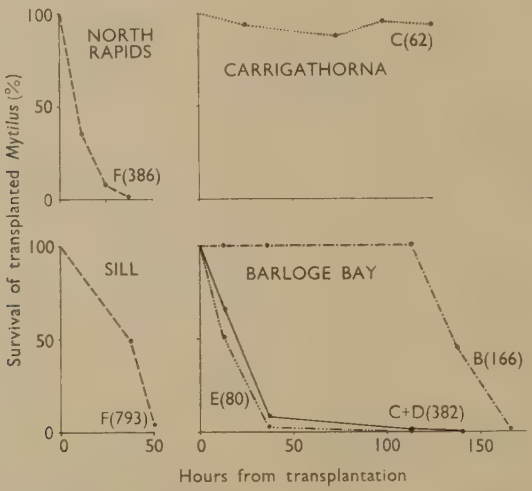

Fig. 3. Percentage survival of small mussels from Carrigathorna transferred with rock substratum to positions in the Rapids, in Barloge Creek, and on the open coast (Carrigathorna). See legend of Fig. 2.

prevented us from reaching the block after 125 h. On 14 September 1958 the block was found to have been moved by the sea into another deeper rock pool, where it was secure but submerged. The largest of the four groups of *Mytilus* affixed to it (thirty-one specimens) remained completely intact, but the other mussels had almost all gone, giving a survival of 51 % since 20 July, the date of placing.

Large *Mytilus* (from the north end of the lough) disappeared quite quickly from all the lough stations except in extreme shelter at East Goleen, where they occur naturally; there was also some slight survival at Glannafeen Beach, discussed below. Once again, predators must have been responsible for their disappearance. The clumps of large *Mytilus* in East Goleen have some small *Mytilus* among them, and there can be little doubt that these escape predation because of the protection afforded by the large ones. Thus *Mytilus* survives as a community even though it

is vulnerable in the younger stages. We must presume that predators which can attack large *Mytilus* in other parts of the lough are absent or ineffective in the region of East Goleen.

Many of the *Mytilus* placed at East Goleen survived until September. The percentage survival after 57 days was 79% for level B (*Fucus spiralis* zone), 71% for C (upper *Ascophyllum* zone), 79% for D (lower *Ascophyllum* and *Fucus vesiculosus* zone), and 49% for F (sublittoral). Thus for the large *Mytilus* from the north end of the lough the heaviest loss occurred sublittorally. Sixteen empty but undamaged shells were found in the sublittoral groups, and there were two *Marthasterias glacialis* upon one of the groups. We have little doubt that *Marthasterias* was responsible for the sublittoral losses, and it is possible that this predator alone would be sufficient to prevent the establishment of *Mytilus* sublittorally in the Goleen.

We do not know why *Mytilus* is confined to the lowest part of the littoral in the Goleen and at the north end of the lough. The groups of large *Mytilus* in the upper *Ascophyllum* zone (C) suffered no loss at all between the end of July and our visit on 6 September, even though *Mytilus* does not occur naturally in the Goleen at this level. It is possible that without splash the conditions are unsatisfactory for settlement or early growth.

The large *Mytilus* placed in the upper *Ascophyllum* zone (C) of Glannafeen Beach survived better than those placed at this level at other stations except East Goleen. On 8 September 82% survived in this zone, and 17% in zone D, but none at other levels. Some pieces of broken *Mytilus* shell were found in zone C. We think that *Portunus puber* is less likely to forage in the littoral region where the shore slopes gently, as this would involve a longer excursion from its usual sublittoral habitat.

PREDATORS OF *MYTILUS*

Slabs of rock covered with *Mytilus* were dislodged with hammer and chisel from Carrigathorna on 19 July, and placed (without cementing) in groups at a series of levels from the *Pelvetia* zone to the shallow sublittoral on the east side of the Goleen and at Glannafeen Quay. The position chosen at the Goleen was on the south side of a very small quay made of loose stones, itself near the south end of the 'East Goleen' station of 1955 (Ebling *et al.*, in press). The *Mytilus* were examined about every 40 min for predators, the series of observations being continued over a period of 53 h; at the end of this time a north-westerly wind made the water cloudy, and the experiment was discontinued. Altogether many thousands of *Mytilus* were placed at each station for this experiment, so that the supply was not seriously diminished by predation during the course of the observations. The quay at each station afforded good access for observation, approach was made over land to avoid disturbance, and a view box was used when required. At night electric torches were shone into the water, and the predators appeared undisturbed over the brief period necessary. A record was kept of the numbers and kinds of animals seen visiting mussels at each level.

The crabs *Portunus puber* and *Carcinus maenas* broke up and devoured many mussels during the course of this experiment. After the end of the experiment a fairly large specimen of the edible crab, *Cancer pagurus*, was seen feeding on the mussels off Glannafeen Quay. During the experiment a few *Marthasterias glacialis* also attacked the mussels. Very many prawns visited the mussels, especially when crabs were feeding, and some were seen to seize fragments of mussel, others to pick up and drop small unopened but detached mussels. A collection of prawns and shrimps, made subsequently with nets and traps off Glannafeen Quay, consisted mainly of *Leander serratus* with a few *L. squilla*. We may assume from their size that almost all the prawns and shrimps reported were in fact *L. serratus*. Gobies and wrasse also visited the mussel patches and nibbled over them as though scavenging. A single *Asterina gibbosa* visited the mussels at Glannafeen Quay.

The results for crabs and prawns are summarized in Fig. 4. Intertidal and sublittoral visits are shown separately. For *Portunus*, *Carcinus* and prawns, there was a strongly marked maximum at nights. Prawns were plentiful at both stations, but though both species of crab were seen at each station, *Carcinus* was much more plentiful at East Goleen and *Portunus* much more plentiful at Glannafeen Quay. The single *Portunus* seen at East Goleen was very cautious about showing itself. *Portunus* was mainly but not entirely sublittoral, whereas *Carcinus* was more plentiful intertidally. Prawns showed a strong tendency to congregate in the shallowest positions, moving up into the intertidal region as the tide rose. The nocturnal maximum of *Carcinus* and prawns appears to have been curtailed by the fall of the tide. Rhythmic behaviour of *Carcinus* has recently been reported by Naylor (1958).

THE SURVIVAL OF *NUCELLA* IN THE LOUGH

The ability of *Nucella lapillus* from Carrigathorna to survive in the lough was tested in two experiments. In the first, 200 specimens collected on 3 July were placed on 4 July along about 12 m of rocky and boulder-strewn shore on the east side of the Goleen, at a position to the north of but adjoining the East Goleen station of 1955 (Ebling *et. al.* 1959). There was a dense belt of *Mytilus* along this strip of shore in the lower littoral. The *Nucella* were placed on the *Mytilus*. During the following eight days they disappeared entirely from the *Mytilus* zone, and only one *Mytilus* was found to have been attacked by a *Nucella*. A number of broken pieces of *Nucella* shell were found, and one *Nucella* lacked an operculum and appeared to have been partly eaten. The survivors moved up out of the *Mytilus* zone to the *Fucus spiralis* and *Pelvetia* zones and even higher. Some moved into deep crevices where they could not be examined properly. However, most of the high ones dried up within the 8 days, and were dead when last examined. It was not possible to make satisfactory counts over the whole strip of shore, but a section of it about 2 m long was examined over the whole tidal range. Here, of 45 *Nucella* at the start of the experiment, 25 were surviving after 50 h, 25 after

75 h, 19 (some of them inaccessible and possibly dried up) after 122 h, and 9 after 194 h, at which time a further 12 were found dried up and dead.

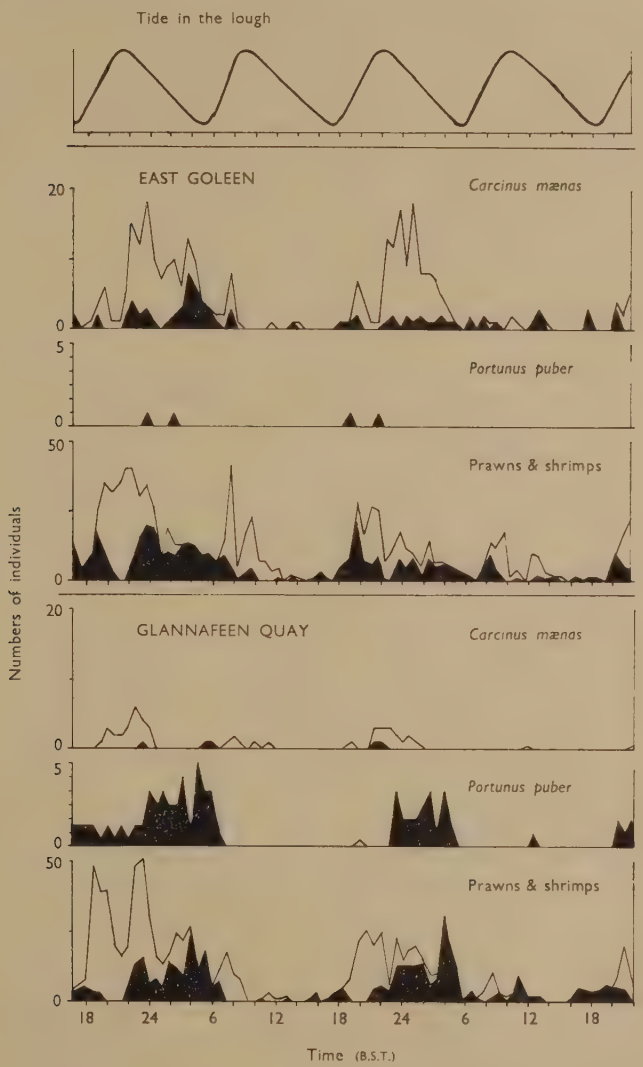

Fig. 4. Numbers of crabs and prawns on beds of small mussels laid in extreme shelter at East Goleen, and in a more open part of the lough at Glannafeen Quay. Black signifies sublittoral, white signifies littoral. *Carcinus maenas* and *Portunus puber* were opening and eating the mussels; the prawns (mainly *Leander serratus*) were merely scavenging.

As it seems possible that the tendency of *Nucella* to move up the shore might be due to some unfavourable chemical condition in the sheltered waters of the Goleen,

we decided in a second experiment to transfer them both to the Goleen and to a site in the open lough where such conditions would be less extreme. In this second experiment *Nucella* were collected at Carrigathorna on 12 July, marked with Indian ink, and placed 5 h later, 100 at East Goleen on the same 2 m strip of shore as above, and 100 at The Slab on the south shore of the lough. The Slab is a steep smooth rock slope with some nearly horizontal crevices, which is about 7 m wide, and is sharply marked off from the adjacent shore. It has a belt of barnacles (*Chthamalus stellatus* and *Balanus balanoides*) in the lower littoral but no *Mytilus*. The *Nucella* were placed in the *Mytilus* zone at East Goleen and at the same level (or in some cases a little higher because of convenient crevices) at The Slab. In all cases the *Nucella* were placed so that they could grip the substratum without risk of falling off. The numbers and levels of survivors recorded at intervals over a period of 16 days are shown in Table 1.

Many pieces of broken *Nucella* shell were found at both stations, and it is likely that the heavy fall in numbers during the first 24 h was due largely to the action of predators. A *Nucella* apparently partly eaten and with its operculum missing was found in the shallow sublittoral at The Slab. Most of the survivors had moved up

Table 1. *Numbers of* Nucella lapillus *surviving after transference on 12 July*

	Hours from start of experiment						
	0	24	49	148	220	300	384
The Slab	100	65	62	46	32	21	23
East Goleen	100	21	10	6	5	5	2

to the upper half of the littoral region, many to the *Pelvetia* zone and a few even higher. There was heavy rain in the last few days of the experiment. A number of those high up at The Slab became swollen so that the body protruded from the shell, and Collembola crawled over some of these.

In a third experiment, carried out on 7 September 1958, a considerable number of *Nucella* were collected at Carrigathorna and placed in the shallow sublittoral at East Goleen Quay and at Glannafeen Quay at about 1945 h, for observation of possible predators. Unfortunately a north-west wind clouded the water at Glannafeen Quay and prevented observation there, so that the following remarks refer only to East Goleen. At 2045 h a solitary *Carcinus* picked up a *Nucella* and carried it under cover. During the next 2 h many more *Carcinus* emerged from cover and captured *Nucella*. One large *Carcinus* held a *Nucella* from which the operculum was missing and tore the flesh with its chelae. Another was seen to tear a *Nucella* behind the operculum. In no case did we see a *Carcinus* break the shell of a *Nucella*. The next morning many severely damaged empty shells of *Nucella* were found in the experimental area, but we do not know how the shells were broken.

The occurrence of *Nucella* requires reasonable freedom from predators, a supply of suitable food, and adjustment of behaviour so that the animals will stay at a suitable level on the shore. We believe that at East Goleen and at The Slab

predators are sufficiently numerous to destroy a population of *Nucella*. Food is available, *Mytilus* at East Goleen Quay and barnacles at The Slab. At both stations the food is confined to the lowest part of the intertidal region, in contrast to Carrigathorna where barnacles and mussels occupy a much larger proportion of the littoral. Nevertheless, *Nucella* can live sublittorally, as on the Sill, and it can live intertidally in the lough as on the north side of Castle Island. It also occurs intertidally on the Rapids Quay (Renouf's Bay to Sill, Fig. 1), where the tidal conditions are much as in the lough. Clearly its behaviour can be adjusted to the tidal conditions of the lough, and it can even live permanently immersed. Possibly it enjoys a relative immunity from predators in the Rapids because of the strong current and on the north side of Castle Island because of other special conditions. For instance, in the area of its occurrence on Castle Island there is a gravel substratum and a dense overlying canopy of *Ascophyllum*; we found only a few small *Carcinus*.

GENERAL CONCLUSIONS

In tests of predation, it is important not to offer the potential victim in an abnormally vulnerable condition. In our experiments the mussels were transferred in clumps together with their substratum and were presented with negligible disturbance. The potential predator had to approach the mussels under natural conditions on the shore and either break them up *in situ* or pull them off and then break them up in a convenient place. There is no doubt that powerful predators are present and ready at the places where in fact *Mytilus* has failed to establish itself, and that these are effective throughout the potential *Mytilus* zone. Whether or not these particular predators ever play a serious part in restricting the distribution of *Mytilus* we cannot tell. It is possible that all the mussels which might live in these places are destroyed at an early age, soon after settlement or even before. Nevertheless, it is relevant that even if they could settle and grow to a substantial size, they would still suffer very severely from the predators revealed in our experiments.

On the open coast *Mytilus* is sufficiently in balance with its predators (including *Nucella*) to survive throughout a season. Possibly wave action restricts the size attained. In moderate shelter, and everywhere sublittorally, predators are sufficiently numerous and powerful to prevent *Mytilus* from becoming established. Between tide marks, in the most land-locked situations *Mytilus* grows to a considerable size on steep rock faces, and even on horizontal ledges where the general slope is nearly vertical. It is possible that difficulty of access, together with some unfavourable physical or chemical condition associated with extreme shelter, protects the mussels from their predators. We may suppose that without this combination one or other predator will prevail. *Carcinus* is very plentiful in the Goleen, close to where *Mytilus* grows, and is probably responsible for the removal of small test *Mytilus*, but it evidently fails to destroy sufficient of the large ones to break up the natural community, at any rate where the shore is steep. The devil crab, *Portunus puber*, powerful and perhaps more agile on a steep shore, is

much less common in the Goleen, and we may suspect that this scarcity is a necessary condition for the survival of the *Mytilus*. The starfish *Marthasterias glacialis* slowly but steadily eliminates mussels placed sublittorally in the Goleen. We have not investigated the feeding habits of the sea urchin, *Paracentrotus lividus*, abundant in many parts of the lough. It visited mussels placed sublittorally at East Goleen, but was not seen to attack them. Other smaller predators may destroy sublittoral *Mytilus* in the younger stages. Newcombe (1935) has shown that *M. edulis* will survive and flourish sublittorally in the Bay of Fundy if protected from predators.

Nucella lapillus, the most conspicuous predator of *Mytilus* on the open coast, is unable to establish itself on *Mytilus* in the lough. It is subject there to predators from which it is presumably safe on the open coast, among them *Carcinus maenas*, which also attacks *Mytilus*. It occurs intertidally on barnacles on the Rapids Quay, and sublittorally on *Mytilus* on the Sill where presumably it is less liable itself to be attacked and eaten. It also occurs as a predator of *Cardium edule* at Northwest Castle on the north shore of Castle Island; but here it seems to occupy a different and unusual ecological niche, presumably brought about by unusual conditions, which possibly restrict its enemies and protect it from them.

A quite extensive bed of rather small *Mytilus* was observed in July 1948 on those parts of the Sill most exposed to current; there were also many *Nucella*. Since then this bed has disappeared, and in July and September 1958 *Mytilus* was confined to the interstices of the holdfasts of laminarian seaweeds; there were still a number of *Nucella*. It is quite possible that the population of *Mytilus* on the Sill undergoes cyclical changes as a result of the predatory action of *Nucella*, as described by Fischer-Piette (1935), so that periodically *Mytilus* might be eliminated from the open rock and only survive where it is inaccessible. At other times it might repopulate the open rock partially protected from its other enemies by the strong current.

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SUMMARY

1. Mussels (*Mytilus edulis* L. and *M. galloprovincialis* Lmk.) are abundant intertidally in the Lough Ine area on the open coast and on steep rock faces in extremely sheltered parts of the lough.

2. Small transplanted mussels disappeared except on the open coast. Large transplanted mussels survived in extreme shelter but not elsewhere in the lough.

3. Mussels strewn intertidally and in the shallow sublittoral in the lough were attacked at night by the crabs *Carcinus maenas* and *Portunus puber*, and many were destroyed within a few days.

4. *Carcinus* attacks small mussels, but does not seriously molest the large mussels found in extreme shelter. *Portunus puber* destroys large and small mussels, but is very scarce in extreme shelter.

5. Clumps of large mussels placed sublittorally in extreme shelter were destroyed gradually by the starfish *Marthasterias glacialis*.

6. In the Lough Ine area *Nucella lapillus* is abundant on the open coast but absent from the *Mytilus* belt in extreme shelter. On transfer to the lough, many *Nucella* disappeared rapidly, and the remainder moved up to the *Fucus spiralis* and *Pelvetia* zones, or even higher, where many dried up or became swollen with rain water.

7. Mussels are remarkably tolerant of extreme conditions of the inanimate environment. They are probably controlled at Lough Ine by interacting predators which are themselves more sensitive to various physical and chemical conditions, such as wave action and stagnation or low salinity.

8. Predators other than those discussed here, acting on the younger stages, may well play an important part in this control.

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THE NATURAL MORTALITY OF *ERIOISCHIA BRASSICAE* (BOUCHÉ) (DIPTERA, ANTHOMYIIDAE) DURING THE EGG STAGE OF THE FIRST GENERATION

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(With 4 Figures in the Text)

In an earlier paper (Hughes & Salter 1959) evidence was given of the primary importance of the egg mortalities in the natural control of the first generation populations of *Erioischia brassicae*. Detailed studies of these mortalities were impossible because of the limitations of the technique for estimating the total number of eggs laid in the soil around the host plants. With this method the soil within 5 cm of the host plant stem was removed to a depth of 2 cm and replaced with fresh soil to bring the area back to normal. The fresh soil was exposed to oviposition by *E. brassicae* for a standard period, and then the soil was removed again and the eggs present in it were counted after separation from the soil by flotation in water. The number of eggs counted was assumed to be the number laid during the period of exposure and the total of a series of consecutive counts made throughout the oviposition period was taken as the total number of eggs laid.

The demonstration of substantial daily egg losses caused by predation (Wishart, Doane & Maybee 1956) showed that egg counts made after a few days' exposure of fresh soil around the host plants would record the number of eggs laid during that period less the number eaten by predators. In other words, if predation were taking place, egg counts made in this way would always underestimate the total number of eggs laid. Later in this paper a description will be given of a modification of Wishart's technique for demonstrating egg losses, which has been used at Wellesbourne, and has again confirmed the existence of substantial egg losses. Since egg losses have been shown to be considerable it has become clear that egg counts made after the same time interval are only directly comparable if the level of predation is similar. Egg counts made after different time intervals can only be directly compared if there is no appreciable significant predation. To avoid the consequences of this experimental error, day by day estimates of the egg loss are required so that the actual number of eggs laid can be calculated from the number counted.

EVIDENCE OF EGG PREDATION AT WELLESBOURNE

Among the insects which occur on the soil around brassica crops, there is a group of beetle species which may prey on the eggs of *E. brassicae*. Feeding experiments carried out at Wellesbourne each year from 1954 to 1958, in which

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the eggs were presented to captive beetles, suggested that the following species were particularly ready feeders on this type of food.

Bembidion lampros (Herbst.)	*T. quadristriatus* (Schrank)
B. litorale (Olivier)	*Aleochara bipustulata* (Linnaeus)
B. quadrimaculatum (Linnaeus)	*A. bilineata* (Gyllenhal)
Trechus obtusus Erichson	*Xantholinus glabratus* (Gravenhorst)

Allied species of *Bembidion* and *Aleochara* are recorded as important egg predators of *Erioischia brassicae* in Canada (Wishart, Doane & Maybee 1956). Of the species listed above only *Bembidion lampros, Trechus quadristriatus* and *Aleochara bipustulata* occur in sufficient numbers at Wellesbourne to be worthy of detailed study.

The presence in the field of beetles which are known to feed in the laboratory on the eggs of *Erioischia brassicae* is not in itself evidence of field predation, however,

Fig. 1. Eggs from field collections showing characteristic predator bite marks.

but some evidence of naturally occurring predation is seen in the characteristic features of partly eaten eggs occasionally found in the field. These three species of beetle normally all chew the chorion of the egg into an unrecognizable mass as they eat the egg contents, but just occasionally a chorion is left in a recognizable form which shows characteristic bite marks (Fig. 1). These damaged eggs are readily found during laboratory feeding experiments where the beetles are disturbed, and the specimens are comparable in every way to those found in the routine egg counts from the field. Other evidence of egg predation is the demonstration of egg losses in the field. Wishart, Doane & Maybee (1956) stained *E. brassicae* eggs with Bengal Rose solution and then placed these marked eggs in groups of ten in suitable positions around randomly selected host plants. The marked eggs that remained after 24, 48 and 72 h were collected and counted. During these experiments egg losses of the order of 20 to 50% occurred daily.

A similar technique was used at Wellesbourne, except that the eggs were unmarked. Groups of ten freshly laid eggs were placed about 5 cm from the stem

of each of ten randomly selected plants on about 1 cm² of smooth soil between two partially buried stones, over which a third flat stone was placed. These caches of eggs were exposed to field predation for 24 h and then the loss of eggs was recorded. The results of five such 24-h exposures of 100 eggs during June 1958 are given in Table 1, an average of 42% of the eggs being lost every day. There is no evidence in this data to suggest that the losses were associated with a particular plant or cache. However, cases of high numbers of eggs eaten per group seem to occur more frequently than the normal (binomial) expectation, for the same mean value. This difference of distribution suggests an agent which is more likely to remove a large number of eggs from a group of ten than would be expected on the hypothesis of chance removal. The statistical significance of this observation can be determined by calculating χ^2 for the difference between the observed and the

Table 1. *Egg losses after 24 h exposure of a group of ten eggs near each of ten host plants*

Figures give the number of eggs eaten out of each group of ten

Plant number	Experiments					Total eggs eaten per plant
	a	*b*	*c*	*d*	*e*	
004	10	4	0	5	0	19/50
104	3	10	3	10	0	26/50
204	0	6	8	0	2	16/50
304	4	7	10	6	4	31/50
404	6	9	3	1	3	22/50
504	7	6	1	0	1	15/50
604	8	10	7	0	0	25/50
704	0	1	0	3	10	14/50
804	4	5	9	3	1	21/50
904	9	6	2	3	1	21/50
Total eaten	51	64	42	31	22	210/500

expected variance of the losses per group; the value is obtained from the formula:

$$\chi^2 = \frac{\Sigma(x-\bar{x})^2}{n\hat{p}\hat{q}}$$

where $\bar{x}$ is the mean loss per plant, n the number of observations, $\hat{p}$ the mean probability of an egg being eaten and $\hat{q}$ the mean probability of it not being eaten. The values of χ^2 obtained for the data of Table 1 are 44·0, 74·1, 53·5, 38·7 and 43·3 for experiments *a*, *b*, *c*, *d* and *e* respectively. The chance of similarity between the observed and expected results is less than 1 in 1000 in every case.

Dr B. Mitchell has described (personal communication) how the locomotory behaviour of both *Bembidion* and *Trechus* individuals changes after they have eaten an egg of *Erioischia brassicae*. The predators no longer move in more or less straight lines but for a period of several seconds they perform a series of tight turns before they resume normal motion. This behaviour usually means that any nearby eggs are quickly located. In laboratory experiments, once a group of eggs is discovered, the beetle usually remains there until the number of eggs in the

group is so reduced that even the turning movements are unlikely to increase the chance of contact. A predator of this type might well give rise to a distribution of egg losses similar to that of Table 1.

There is some doubt as to whether the average egg loss per day, shown by techniques similar to Wishart's, truly reflects the natural predation of the egg population as a whole. Of all the factors involved in natural predation only the number of available predators is common to the experimental model as well. While there is, of course, a certain similarity between the site where the eggs are placed and a natural oviposition site under a host plant, the eggs have either to be marked or placed in positions where additional egg laying by *E. brassicae* is unlikely. The washing of the eggs during their separation from the soil may affect any chemotactic responses of a predator. Furthermore, the number of eggs used is limited, and if all are eaten there is no means of knowing how many would have been eaten if more had been there. The special behaviour of the predators which makes it easier for them to detect and eat all of a group of nearby eggs makes this uncertainty important. The natural egg population is limited, too, but this limit would vary from plant to plant and from day to day. These unsatisfactory features would seem to be common to all indirect methods which make use of artificial egg populations. The only way of avoiding these difficulties would be to estimate the egg losses directly on the natural egg population, possibly from the egg counts themselves.

EGG COUNTS

(*a*) *The effect of predation*

Since the egg counts consist of the number of eggs laid less the number eaten by predators, the proportion eaten reflects the level of predation. The following analysis of the effect of predation on egg counts was made to investigate the possibility of estimating egg survival directly from the egg counts.

Consider a large population of *Erioischia brassicae* such that random variation is small enough to be ignored. Let $x_1, x_2, x_3, \ldots x_n$ be the number of eggs laid on days 1, 2, 3, ... n, $q_1, q_2, q_3, \ldots q_n$ be the proportion of eggs not eaten on days 1, 2, 3, ... n, and $c_1, c_2, c_3, \ldots c_n$ be the number of eggs remaining after days 1, 2, 3, ... n. The number of eggs remaining on each day (c), can be defined in terms of the number laid and the proportion surviving each day, as follows:

$$
\begin{array}{lllll}
\text{After day 1} \ldots c_1 = x_1q_1 & & & & \\
\text{day 2} \ldots c_2 = x_1q_1q_2 & +x_2q_2 & & & = q_2(c_1+x_2) \\
\text{day 3} \ldots c_3 = x_1q_1q_2q_3 & +x_2q_2q_3 & +x_3q_3 & & = q_3(c_2+x_3) \\
\text{day 4} \ldots c_4 = x_1q_1q_2q_3q_4 & +x_2q_2q_3q_4 & +x_3q_3q_4 & +x_4q_4 & = q_4(c_3+x_4)
\end{array}
$$

Soil collected from around the plants after exposure to oviposition will contain the remaining eggs (c). Thus egg counts made after two days will be equivalent to c_2, after three days equivalent to c_3, etc.

Some of the features of this system can be seen more easily if the number of eggs

laid each day and the proportion which survive each day's predation are assumed to be constants; in other words if there are only single values of x and q. This simplified mathematical model can be written: $c_1 = x(q)$, $c_2 = x(q^2+q)$, and generally $c_n = xq(1-q^n)/(1-q)$.

For example if eight eggs are laid each day and half of them survive each day, the numbers surviving on eight successive days will be, on this model, 4, 6, 7, 7·5, 7·75, 7·88, 7·94 and 7·97 respectively. It will be seen that the increase of the value of c becomes less and less each day until it approximates to a constant value given by the formula $c_\infty = xq/(1-q)$. The errors that arise by comparing egg counts made after different time intervals can now be illustrated. Making the same assumptions as above (eight eggs laid per day of which half survive each day), if counts are made every 2 days six eggs will be counted on each occasion, making a total of twenty-four over an 8-day period; but if counts are made every 4 days 7·5 will be found at each count, making fifteen for the same 8 days. The discrepancy of 38% results solely from taking the counts at longer intervals and is a function of the survival rate alone, being independent of the number of eggs laid so long as this number is constant. A more general statement of this effect is that if the number of eggs laid is constant, the ratio of an average 4-day count to an average 2-day count is 5 : 4 if the proportion of eggs surviving each day is half the number present. For the rest of this paper ratios will be given as the equivalent decimal fraction, in this case 1·25.

The 4-day : 2-day egg count ratio will vary for different proportions of eggs surviving predation, and its values can be calculated from the formula: (average 4-day count)/(average 2-day count) $= (q+q^2+q^3+q^4)/(q+q^2) = 1+q^2$. When the survival ranges from 0 to 1 the value of this ratio ranges from 1 to 2, as shown in Fig. 2. If the survival q is unknown it would be possible to interpolate an observed value of the 4-day : 2-day egg count ratio in Fig. 2 and so estimate q.

The ratio of the average 4-day to the average 2-day egg count can be determined for the same field population of *E. brassicae* eggs but whether this ratio can be used to estimate the daily survival of eggs depends on whether the conditions of the original mathematical model can be assumed. These conditions were that the number of eggs laid on each day and the proportion of eggs surviving each day are both constants. Both oviposition by *E. brassicae* and predator activity are probably related to the prevailing weather conditions. The method of oviposition and the long egg-laying life of *E. brassicae* females tend to stabilize the rate of oviposition per plant unless the weather interferes. Short periods of stable weather do occur and during such a period both the predator activity and the oviposition will probably be approximately constant from day to day. If the ratio can be calculated separately for short periods of time, there is a chance that at least some of these periods will have stable weather conditions. The shortest period over which 4-day and 2-day egg counts can be compared is 4 days, the ratio of the 4-day count to the average of the two 2-day egg counts being calculated. Another assumption implicit in the mathematical model is that individual eggs remain equally accessible to the predators throughout the incubation period. This is

probably true except under conditions of heavy rain, the effect of which is discussed later.

Besides the basic assumptions of the model, the practical assumptions made when estimating the ratio of the 4-day and 2-day counts must be considered. The standard deviation of an egg count made on ten plants is about 10% of the mean. This rather high standard deviation results from the occasional large number of eggs laid on an individual plant. To allow the usual statistical techniques to be used on such data they have to be 'normalized' by using the appropriate transformation log $(x+1)$. More important is the difference between the two series of counts in the number of times the soil is disturbed. It is necessary to assume that

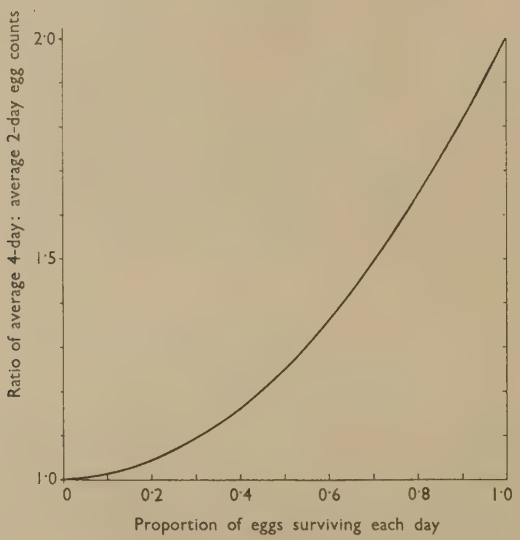

Fig. 2. The variation of the 4-day : 2-day count ratio with different proportions of eggs surviving each day.

over any one 4-day period, the replacement of soil after the first 2-day egg count will not increase or decrease the likelihood of eggs being laid on that group of plants during the next 2 days, compared with the undisturbed soil of the plants used to make the associated 4-day egg count. This assumption was tested using two similar groups of plants. One group of plants was cleared of eggs and the soil replaced in the routine fashion. A cage of screen material was then placed over each plant to prevent eggs being laid, but allow normal weathering of the soil around the plants to occur. These cages were removed after 2 days and the plants exposed to oviposition for 2 days more. After this period an egg count was made and compared with a routine 2-day egg count covering the same period of oviposition but on the second group of plants. Any effect of soil treatment is swamped by the large variation in the number of eggs laid around individual plants, and either

series of plants may have the larger total (Table 2). No significant differences between the egg counts on the two series of plants were recorded in these experiments and therefore the egg-counting techniques used will give in practice a reasonable estimate of the 4-day : 2-day egg count ratio.

(*b*) *Four-day and two-day egg counts in* 1958

In 1958 a routine was established for taking three series of egg counts, one series taken after consecutive 2-day periods and two series after consecutive 4-day periods. The two 4-day series were out of phase with each other by 2 days, the idea being that there would in this way be more chance of getting a 4-day period coincident with a period of settled weather. The weather in the spring of 1958 seemed to run in cycles of from 4 to 6 days, so that there should have been roughly

Table 2. *Numbers of eggs laid during a 2-day period, when the soil was disturbed either 4 days or 2 days before the count*

Plant number	Soil disturbance			
	4 days before		2 days before	
	Expt. A	Expt. B	Expt. A	Expt. B
0	3	1	6	26
1	14	15	4	1
2	11	34	18	3
3	3	11	5	14
4	7	18	3	14
5	3	4	4	12
6	18	23	25	47
7	12	1	11	4
8	14	19	9	7
9	0	16	19	3
Total count	85	142	104	131

an even chance of any particular 4-day period occurring during stable weather conditions. The records of these egg counts for the first generation of *E. brassicae* in 1958 are shown in Table 3. Before the 4-day : 2-day count ratio is calculated the data are transformed to logarithms so as to normalize them and give a better estimate of the mean values. This is equivalent to estimating the geometric mean number of eggs per plant, given by the back transformation of the mean logarithm of each egg count. These geometric mean numbers of eggs per plant are given in the table and are used to calculate the 4-day : 2-day ratio.

ESTIMATING THE TOTAL NUMBER OF EGGS LAID

An estimate of the number of eggs laid is calculated in three steps; calculation of egg survival over individual 4-day periods; relating these measures of egg survival to the average predator population during the respective 4-day periods, and using this relationship and the daily predator count to give a daily measure of egg

survival; and using the 2-day egg counts and the daily measure of egg survival to calculate the number of eggs laid.

The 4-day : 2-day egg count ratio is readily calculated using the formula: $R = 2(4\text{-day count})/(1\text{st 2-day count} + 2\text{nd 2-day count})$. Calculated ratios for the present data are shown in Table 3. Substitution of these ratios in the formula $R = 1 - q^2$ gives estimates of the average daily survival of eggs over the 4-day periods. These values are given in the last column of the table. Only half the calculated ratios can be interpolated on Fig. 2 because the remainder have values outside the limits of 1·00 and 2·00. These anomalous ratios cannot be directly interpreted as they imply that more than all or less than none of the eggs survived each day. There is no doubt that some of these anomalous

Table 3. *Numbers of eggs counted at consecutive 4-day and 2-day intervals from sample groups of ten cabbage plants, with the geometric mean numbers per plant and the calculated 4-day : 2-day egg count ratio*

Means are geometric mean numbers of eggs per plant.

	4-day intervals				2-day intervals		Ratio 4-day : 2-day	Estimated survival (q)
	Series A		Series B					
	Count	Mean	Count	Mean	Count	Mean		
7 May	–	–	–	–	157	11·9	–	–
9 May	178	13·7	–	–	140	9·8	1·26	0·51
11 May	–	–	213	15·7	169	11·2	1·47	0·69
13 May	227	15·9	–	–	195	16·7	1·14	0·37
15 May	–	–	122	8·3	264	19·4	0·46	–
17 May	156	10·2	–	–	61	3·4	0·89	–
19 May	–	–	125	9·1	160	12·3	1·28	0·53
21 May	378	31·1	–	–	135	8·9	2·94	–
23 May	–	–	367	30·4	89	6·8	3·88	–
25 May	138	11·8	–	–	141	8·9	1·50	0·71
27 May	–	–	161	14·3	126	8·0	1·69	0·83
29 May	213	18·4	–	–	157	8·0	2·29	–
31 May	–	–	208	13·9	65	5·5	2·06	–
2 June	85	7·1	–	–	49	3·2	1·63	0·79
4 June	–	–	134	8·8	26	1·5	3·74	–
6 June	48	2·8	–	–	34	2·2	1·52	0·72
8 June	–	–	32	2·1	74	4·2	0·64	–

ratios occur by chance; for example those ratios for the 4-day periods ending 21 and 23 May are greater than 2·00 probably because of the suspiciously low 2-day egg count obtained on 21 May. However, most of these anomalous ratios occur in those 4-day periods when the weather changed abruptly half-way through. If the rate of oviposition goes from high to low, a ratio of less than 1·00 can occur, while if the rate changes from low to high ratios of more than 2·00 are probable. A characteristic feature of several of the periods when anomalous ratios occurred was a spell of very intense rainfall. Since *Erioischia brassicae* females lay their eggs in soil crevices and under soil crumbs, the assumption of continuous accessibility of the eggs to predators may not be valid if the soil surface structure is broken down by heavy rain. To test this hypothesis laboratory experiments were carried

out to find out if rain is likely to seal eggs from predation. The first experiments were designed to show whether eggs covered by a thin layer of soil were less likely to be eaten than exposed eggs. Dishes containing a flat soil surface were set up with 100 eggs spread evenly over the area of soil. In half the experiments ten predators were allowed to feed on these exposed eggs for 24 h. In the rest a 'one-grain' layer of sand was spread over the eggs before the predators were allowed to feed. The results of these experiments are given in Table 4 and they show that more than twice as many uncovered eggs are eaten compared with those covered.

Such clear-cut results were more difficult to repeat in experiments using more natural conditions but less controllable in design. Young turnips grown in 13 cm diameter plant pots were exposed to oviposition by a caged population of *E. brassicae* adults reared in an insectary. After 24 h the plants were removed from the cage and the soil surface was divided into quadrants by vertical plastic screens. Alternate quadrants of soil were sprayed with fine droplets of water to

Table 4. *The effect on predation of covering eggs with a 'one-grain' layer of sand*

Figures give the number of eggs remaining out of 100 exposed to predation for 24 h by ten specimens of the predator.

Experiment	Predator *Bembidion lampros*		Predator *Trechus quadristriatus*	
	Uncovered	Covered	Uncovered	Covered
i	29	76	3	39
ii	19	63	6	73
iii	10	58	14	52
iv	26	77	29	41

simulate rain. The plastic screens were then removed and ten predators (*Bembidion lampros*) were confined to the soil surface by a polythene cylinder fitting closely around the plant pot. After 24 h the beetles were taken off and the soil of each quadrant was removed separately and the number of eggs present in each quadrant was recorded. In analysing the results of these experiments the chief difficulty was that the numbers of eggs laid on each plant was unknown and probably different in every case. Table 5 gives the results of thirteen such experiments which, if taken as a whole, clearly indicate the protection of eggs from predation as a result of the watering. The sealing of eggs from predation as a result of intense rainfall could probably account for some of the ratios being higher than 2·00 as seen in Table 3.

(*b*) *Relating egg survival to the predator population*

Mitchell (1958) made daily records of the numbers of predatory beetles caught in fifty pit traps placed near the stems of cabbage plants on the same plot from which these egg count data were derived. Mitchell has pointed out that a daily pit trap count is a measure of the product of the predator population and its

activity on that day, and is directly related to the probability of a predator reaching a particular point during the 24 h. This type of data is ideal for comparing

Table 5. *The effect of watering on the predation of* Bembidion lampros *on the eggs of* Erioischia brassicae

Figures give the number of eggs remaining after 24 h predation

Experiment	Watered	Unwatered	Experiment	Watered	Unwatered
a	240	211	*h*	100	90
b	74	45	*i*	38	25
c	48	66	*j*	210	62
d	316	191	*k*	125	149
e	249	151	*l*	55	34
f	10	10	*m*	84	57
g	248	190			
		Mean % of eggs remaining		57·5	42·5
				±4·5	

with the measure of predation given by the 4-day : 2-day egg count technique. It is more convenient to compare the proportion of eggs eaten with the predator count; the former being derived as: Egg loss (p) = 1 − egg survival (q). The

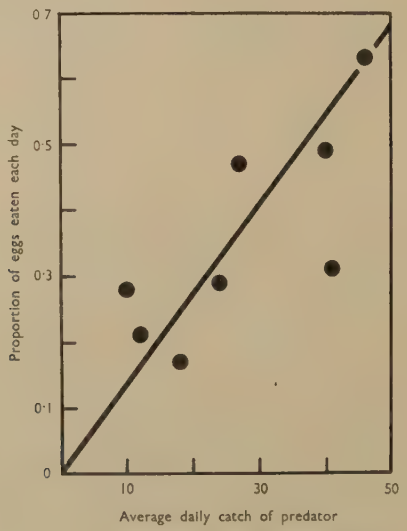

Fig. 3. First generation 1958; the relationship between the proportion of eggs eaten each day and the average numbers of the predator *Bembidion lampros* caught each day in fifty pit traps.

average egg loss for each 4-day period is compared with the contemporary average daily count of predators. The results of this comparison are shown graphically in Fig. 3 and suggest a linear relationship over this range. The best fitting line does

not pass through the origin but the data do not differ significantly from a regression line passing through the origin and the mean point of the data. The hypothetical relationship can therefore be based quite reasonably on the simplest regression equation:

Egg loss (p) = predator count × constant;* $p = 0{\cdot}0136\ P$ (see Fig. 3) or egg survival (q) = $1 - 0{\cdot}0136\ P$.

Table 6. *Estimating the total number of eggs laid on ten plants*

Date (i)	Number of predators (ii)	Egg survival (iii)	2-day egg count (iv)	Number of eggs laid each day (v)
4 May	53	0·28		100
5 May	37	0·50	64	100
6 May	27	0·63		261
7 May	46	0·37	157	261
8 May	46	0·37		237
9 May	42	0·43	140	237
10 May	34	0·54		256
11 May	42	0·43	169	256
12 May†	38	1·00		195
13 May	71	0·03	195	195
14 May†	53	1·00		198
15 May	49	0·33	264	198
16 May	16	0·78		45
17 May	18	0·76	61	45
18 May	38	0·48		213
19 May	36	0·51	160	213
20 May	37	0·50		313
21 May	52	0·29	135	313
22 May	40	0·46		67
23 May†	19	1·00	89	67
24 May†	26	1·00		70
25 May†	11	1·00	141	70
26 May	19	0·74		90
27 May	15	0·80	126	90
28 May	15	0·80		103
29 May	12	0·84	157	103
30 May	12	0·84		42
31 May	12	0·84	65	42
1 June	11	0·85		31
2 June	11	0·85	49	31
3 June	16	0·78		16
4 June	8	0·89	26	16
5 June	8	0·89		20
6 June	7	0·90	34	20
7 June	12	0·84		61
8 June	5	0·93	75	61
9 June	1	0·99		25
10 June	2	0·97	50	25
Accumulated totals for first generation *E. brassicae*, Wellesbourne 1958			2157	4686

† Samples affected by heavy rain—see text.

Since there are daily records of the predator count, a daily measure of egg survival can be calculated from this last equation. The results of these calculations are given in column (iii) of Table 6.

* Recent observations suggest an equation of the type: egg loss (p) = e^{kP}.

(c) Calculating the number of eggs laid

For each 2-day period corresponding to a 2-day egg count, eggs laid on the first day have to survive predation on both days, but eggs laid on the second day only have to survive that day to be counted. The survival of two batches of eggs can be represented as q_1q_2 of the eggs laid on day 1 and q_2 of the eggs laid on day 2 where q_1 and q_2 are the egg survivals on days 1 and 2 respectively. Since the number of eggs counted after 2 days is made up of both these batches of eggs, the average number laid on each day is estimated by (number of eggs counted)/$(q_1q_2+q_2)$. For example, on 17 May 1958 the 2-day egg count was 61; egg survivals on 16 and 17 May were 0·78 and 0·76 respectively; therefore the average number of eggs laid each day was $61/[(0{\cdot}78\times0{\cdot}76)+0{\cdot}76] = 45$. Such estimates of the actual numbers of eggs laid have been calculated for the whole oviposition period, and are given in column (v) of Table 6. Heavy rain occurred on five occasions before the plants were large enough to provide shelter for the eggs from it, and on these dates complete survival is assumed (these dates are indicated by a dagger in Table 6). The grand total of column (v) in Table 6

Table 7. *Total egg mortalities in the first generations in 1957 and 1958*

	Calculated number of eggs laid per plant	Number of eggs counted per plant	Number of larvae surviving	Total mortality* (%)
1957	405·2	190	39	90·5 (79·8)
1958	468·6	220	25	94·7 (88·6)

* Figures in parentheses from Hughes & Salter (1959).

gives 4686 as the total number of eggs laid near ten host plants. This number is more than twice as great as the number (2157) counted in the 2-day counts.

EGG PREDATION AS A PROPORTION OF TOTAL EGG MORTALITY

Hughes & Salter (1959) used the total of the 2-day egg counts and the number of surviving larvae to calculate a measure of the total egg mortality during the first generation of *Erioischia brassicae* in 1958. In the same paper the total number of eggs counted was also used to measure the total egg mortality in previous years. The total egg mortality can now be recalculated using the number of eggs laid and the number of surviving larvae. Data similar to those of Table 6 are available for the first generation in 1957. The results of the recalculation of the 1957 and 1958 data are given in Table 7.

The probability that an egg will be eaten by predators before it hatches depends on the number of days it is exposed to predation and on the likelihood of survival on each of those days. The length of time an egg is exposed to predation is the same as the incubation period, which can be calculated from the fact that 96 day-degrees above a threshold of 45° F are needed to complete the development of the

egg stage (Hughes & Salter 1959). Daily records of the maximum and minimum temperature at the soil surface below a cabbage plant were used to compute the approximate time taken to hatch, of eggs laid on each day of the oviposition period.

Knowing the number of eggs laid on each day, the length of time they will be exposed to predation and the proportion of eggs which will survive each day, the number of eggs that will survive to hatch into larvae can be calculated. For example, on 22 April 1957 10·5 eggs were laid per plant and 8 days were necessary to complete their development to hatching. Egg survivals on each of the eight days were 0·70, 0·73, 0·55, 0·41, 0·77, 0·71, 0·48 and 1·00 respectively. Egg survival over the whole period is the product of these values, *i.e.* approximately 0·03, so that 0·3 eggs per plant would have survived to hatch on the eighth day.

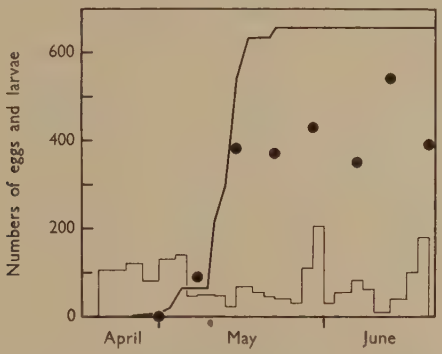

Fig. 4. Comparison of observed and calculated larval numbers hatching from the 1st generation egg population 1957. Dots show observed larval number, heavy line calculated larval number, histogram number of eggs laid per day.

When heavy rainfall interfered with predation the computation was varied slightly. For example on 24 April 1957 11·9 eggs were laid per plant and 9 days were needed to complete their development. Egg survivals on the first 6 days were 0·55, 0·41, 0·77, 0·71, 0·48 and 1·00 respectively. On the sixth day heavy rain sealed the eggs into the soil surface and it was assumed that no further predation occurred. Egg survival over the whole period was therefore taken to be the same as that over the first 6 days, *i.e.* 0·06, so that 0·7 eggs would have hatched per plant. In this way the existence of the eggs laid on each day of the whole oviposition period was followed through, and the number that survived predation calculated. The results of this computation for the first generation of 1957 are shown in Fig. 4 where the predicted hatch is compared with the observed numbers of larvae in soil samples containing the main root systems of ten host plants.

The timing of the predicted hatching of the larvae is a very good fit, but the number of larvae observed (thirty-nine) is only about two-thirds of the number

predicted (sixty-six). This result may be explained in two possible ways. The predation may be accounting for something less than the total mortality; predation mortality can be calculated to be 85·7% as compared with the total mortality of 90·5%. However, in the calculation of the predation mortality, the majority of the eggs which probably survived to hatch into larvae were those sealed from predation by rain. The assumption that no further predation occurs may well not be strictly accurate. Low-grade predation of the sealed eggs could account for the apparent difference between predation mortality and the total mortality. A similar relationship of predation mortality to the total was shown to occur in the 1958 data.

DISCUSSION

The 4-day : 2-day egg count technique has made possible a more accurate measure of the number of eggs laid by *Erioischia brassicae* populations. Other combinations of time intervals could be used without altering the basic argument. These combinations may well be more sensitive, as it is best to have the largest possible difference between the average counts because of their large standard deviation. Other factors, such as the shortest time for the eggs to hatch, usually limit the choice of time intervals.

Table 7 shows that in 1957 and 1958 an almost identical percentage (47%) of the eggs laid were counted. As this result occurred in spite of differences in the lengths of oviposition periods, in the weather conditions and in the intervals between egg counts, it was attributed to chance.

Four possible causes of mortality to be included in the total egg mortality have been put forward (Hughes & Salter 1959). These are egg predation, reduced egg viability, drought effects on newly hatched larvae and the failure of the latter to find the host plant. Of these, egg predation makes up the bulk of the total mortality. Observations on eight samples of 100 eggs brought in from the field showed that the viability ranged from 90 to 100% with a mean value of 96%. This result suggests that the reduced viability of the eggs may account for about a tenth of the unaccounted difference (5%) between predation mortality and the total. Since the majority of eggs which survive are probably those sealed into the soil by heavy rain, there is little chance that dry weather will have much effect on newly hatched larvae. The failure of these larvae to find the host plant could easily account for any remaining mortality.

The results of the calculation of the proportion of egg mortality caused by predation suggest that while the mortality was around 90% in both years, about a further 5% of the eggs could have been eaten by the predators if the latter had been unhindered by heavy rain. The efficiency of predation appears to be modified in three ways by the weather. First, the activity of the predators varies with the weather, which therefore governs the number of eggs they find. Secondly, the length of time the eggs are available to be eaten depends on the prevailing temperature. Thirdly, heavy rainfall may cause the soil to seal the eggs from further predation. The role of the weather and possibly other factors in modifying preda-

tion efficiency makes it impossible to relate directly the absolute population of predators and the total predation mortality.

ACKNOWLEDGMENTS

It is a pleasure to thank Mr D. W. Wright and Mr J. A. Nelder for their encouragement and advice during this work.

SUMMARY

1. Evidence is given of predation of *Erioischia brassicae* eggs on *Brassica* crops by the ground beetle fauna at Wellesbourne.

2. When counts are made of the number of eggs laid, this predation results in an underestimate of the total.

3. A method is described of deriving the average survival of eggs, over a short period of time, by counting the eggs at different time intervals.

4. Predation losses over the short periods are related to contemporary daily trap-catches of predators.

5. This relationship of predation to the daily trap-catch of beetles is used to estimate the probability of egg survival on each day.

6. The probability of egg survival on each day is used in conjunction with the number of eggs counted to estimate the total number of eggs laid.

7. Calculations show that egg predation is the major cause of egg mortality, accounting for over 90% of the losses in the 1957 and 1958 first generations of *E. brassicae*.

8. The role of the weather in modifying predation efficiency is discussed.

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THE DIET OF THE FOX SINCE MYXOMATOSIS

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(With 1 Figure in the Text)

Early in 1954 myxomatosis began to spread from its original centres in Kent and Sussex so that over many areas rabbits were no longer present in the countryside. Work by Southern & Watson (1941) suggested that rabbits then accounted for some 55% of fox diet, more particularly in spring and summer. With the sudden removal of its main item of food it was only natural that sheep- and other farmers, poultrymen, and all those concerned with game preservation should have been apprehensive lest the fox might radically change its diet at their expense. Accordingly, it was arranged that bodies of foxes should be sent to the Infestation Control Division, the first ones arriving in January 1955. It proved possible to have only seventeen foxes before the arrival of myxomatosis, so that no detailed comparisons could be made of the position before and after this disease became established. Counties were selected to represent as many different types of topography and land utilization as possible, but it was not possible to arrange for carcasses of foxes to come from all areas. Except for Kent, specimens came mostly through the County Pest Officers, many as a result of shoots organized by various Fox Destruction Societies. A preliminary account of the results obtained after only eighty fox stomachs had been examined was written by Lever, Armour & Thompson (1957) and this is now supplemented by the results obtained from the examination of more than 400 stomachs and 120 droppings or scats.

THE MATERIAL

(*a*) *Sources*

The reason for the preponderance of stomachs was that as the material found in them was less digested than that in the droppings, its identification was easier. It was also decided to record skull and body measurements and gross weights as well as to preserve for further study the reproductive tracts and internal parasites of the fox.

The material for investigation of diet consisted of 420 stomachs (385 adult foxes and 35 cubs) and 123 scats collected in the field. The distribution of this material is given in Table 1 which shows that 40% of the English foxes came from Kent; Westmorland is the only county represented north of a line adjoining the Humber and Mersey. East Anglia, central and northern Wales, the Midlands and south-west England were poorly represented. There is, however, a fairly extensive range in topography from Cornish moors, coastal and old tin-mining areas, woods (New

Forest and Sherwood Forest), downland (west Sussex), and Essex market gardens (Chelmsford). In Wales, the fifty-five foxes from Flintshire and Denbighshire were collected within a period of 13 months. This area comprised farmland (mainly near Hawarden, Rhyl and St Asaph) and extended to the River Dee at Sealand. Hill foxes came from Montgomery and Breconshire. Scotland is represented by twenty-nine adult and six cub stomachs and thirteen scats, from the following highland areas: south Aberdeenshire (Old Deer and Braemar), Banffshire (Ben Rinnes) and Inverness-shire (Cairngorms), and from Argyleshire (Lorne) in the west and a few from Fife and Kinross in the east. The sex ratio was approximately 116·5% (226 males : 194 females); it is impossible to say whether this is a random

Table 1. *Sources of material*

ADULTS	Stomachs	Scats
Bedfordshire	2	–
Berkshire	–	48
Buckinghamshire	3	–
Cheshire	3	–
Cornwall	11	17
Derbyshire	12	–
Essex	23	–
Gloucestershire	4	–
Hampshire	16	16
Herefordshire	4	3
Hertfordshire	2	–
Kent	122	4
Lincolnshire	1	–
Middlesex	2	–
Northamptonshire	3	–
Nottinghamshire	8	–
Oxfordshire	2	–
Somerset	2	–
Surrey	1	4
Sussex	8	–
Westmorland	62	14
Total, England	291	106
Brecon	5	–
Denbighshire	2	–
Flintshire	50	3
Montgomery	5	1
Pembrokeshire	3	–
Total, Wales	65	4
Aberdeenshire	12	–
Argyll	11	–
Banffshire	–	8
Fife	4	–
Inverness-shire	–	5
Kinross	2	–
Total, Scotland	29	13
Total, adults	385	123

CUBS

England 29, Scotland 6, total 35 stomachs; scats 0

Grand total: 420 stomachs, 123 scats = 543 specimens
Sex ratio: males 226 (54%), females 194 (46%)

sample of the fox population. Lund (1959) found 301 males to 250 females (ratio 120%) in Norway. No distinction has been made in this paper between the Scottish race *Vulpes vulpes vulpes* and the English and Welsh *V. v. crucigera*.

(*b*) *Collection*

Most of the foxes had been shot, but in a very few instances from Scotland and Wales snares and traps had been used; gassing in the earths was the method used on only five occasions; all but a few of the cubs were dug out. The carcasses were sent by rail in strong zinc bins and kept in a deep-freeze refrigerator before removal of the viscera. On a few occasions specimens arrived in a putrid condition and had to be discarded without examination. The stomachs were preserved in formalin, mostly for periods of from 1 to 2 months but in some cases up to nearly 2 years before examination. The reception, documentation and preservation of

the material received during 1955 and the first two months of 1956 were carried out by Mr I. Hattingh, who also examined some of the stomachs received from Kent.

(*c*) *Examination*

After the removal and washing of the stomach contents, the finer material was filtered through a $\frac{1}{25}$ in. wire mesh for later detailed examination. Coarser material was dried on hessian strips if it was adequate in quantity, or between sheets of blotting paper if it was very scanty. In stomachs yielding only a trace, everything found was placed in water in petri dishes, the fragments being removed with fine forceps or a pipette. A number of intestines were also available, the rectal contents being the most useful portion. The addition of a few ml of 'Teepol' proved helpful in cleaning very fatty or milky stomach contents. Scats gave nearly $2\frac{1}{2}$ times as many rodent teeth as stomachs and had a higher proportion of other undigested material; presumably this represents remains from several meals. As it was found that the sieve held back such fine remains as small rodent teeth and legs of beetles, this screened material was at first considered satisfactory for studying the diet of such a large carnivore as the fox. Later, however, it was found that the body segments of earthworms had been so rapidly digested that the only traces left were the minute chaetae mixed with grit which passed through the sieve, so this material was also examined.

Sorting of the varied material was much simplified by the use of a wide field head-band binocular enabling teasing out with needles and forceps. Rodent teeth were useful for specific identification of rodents, but bones of larger animals were invariably too splintered to be of much value. Hairs were used to a considerable extent for comparison with a fairly long series of slides made by the writer from known mammals. The hairs were cleaned in carbon tetrachloride and, where dehydration was necessary, immersed in Gurr's 'Dioxan'. Liquid paraffin was often used for temporary mounts. For permanent mounts, dry, cleaned hairs were placed under a cover slip and ringed with transparent nail varnish; this method proved better than mounting in Canada balsam. Casts of hairs were made either on polyvinyl acetate or on fixed photographic plates cut to 3×1 in. The hairs were laid on the moistened gelatine, pressed, dried and stripped away to leave casts. Full details of hair examination are described by Wildman (1954) and Stoves (1957), whose books show the varied structure of the scales present on the cuticle of guard hairs which grow through the weaker under-fur. Not only is there considerable variation in the cuticular scale structure in hairs from different parts of the same animal, but the pattern changes throughout the length of individual hairs.

(*d*) *Recording*

Food items found were entered on punch-cards which, as an economy measure, were issued blank and used with a typed master card. Details of locality, collection date, sex and any other relevant information were also recorded. As a study of the literature suggested that the system used by Scott (1941) was best, the method adopted was to record the various food items by their percentage frequency of

occurrence. This figure denotes the percentage of stomachs in which a particular item occurs as distinct from the relative proportion of each food item to the total items found. Thus, if animal *x* is found in four out of twenty stomachs examined, the percentage recorded is 20%; inevitably this method gives figures which total more than 100%. By the system of relative proportions these four records would be expressed as the proportion of all food items found which if it was twelve would give 33⅓%; in this case the separate figures add up to 100%.

Consideration was given to the use of a system which, by a differential weighting, would allot a higher relative value to such smaller food items as voles compared with larger animals such as rabbits or sheep. Lockie (1959) has shown that, when known food items are fed to captive foxes, the best criterion is the weight of dry faecal undigested material.

CATEGORIES OF FOOD

(*a*) *Mammals*

With the spread of myxomatosis through 1954 and 1955, virtually no rabbits occurred in south-eastern England. This state of affairs was confirmed by examination of fox carcasses from western Kent, where during 1956 lagomorph remains occurred in only 20% of stomachs examined, whereas when myxomatosis receded drastically in the following year the figure rose to 40%. Conversely, in Westmorland, where although myxomatosis had arrived by the end of December 1954 it had not covered the county a year later, the figures for lagomorph remains fell from 28% in 1956 to 17% in 1957 (Table 5). Teeth occurred rather infrequently since heads of adult rabbits seldom appear to be eaten, although teeth and ears of young animals were found on several occasions. Feet also were recovered but leg bones were usually only present as fragments. Hair by itself was therefore used to a considerable extent, as had earlier been done by Southern & Watson (1941), but it is unfortunate that one cannot clearly distinguish guard hairs of rabbit and brown hare. However, tufts of hair from mountain or blue hares were found in scats from foxes living at heights up to 2000 ft in parts of Banffshire and Inverness-shire known to be free from rabbits.

Rodents, other than squirrels, occupied a high place in the diet of the foxes, remains of the field vole (*Microtus agrestis*) being most numerous. Table 2 lists the recoveries of rodent teeth from 245 stomachs and scats containing remains of small rodents. Teeth occur nearly 2½ times as frequently in seventy-five scats as in 170 stomachs, *Microtus* accounting for three-quarters of the rodents represented in both types of material. In the regurgitated pellets of owls and buzzards the palatal area of skulls is recovered more or less entire, often with the mandibles adjacent to it. By contrast, the material from the fox is usually so splintered as to occur in small fragments, the teeth often lying loose.

It is known from live trapping with Longworth traps in various types of vegetation that the bank vole (*Clethrionomys glareolus*) and the wood mouse (*Apodemus sylvaticus*) are extremely abundant animals. The low position of the bank vole in

fox diet may be attributed to the habit of this rodent, referred to by Evans (1942), of frequenting somewhat dense patches of cover such as bramble thickets or bracken. As a result, the fox may well neglect the bank vole for the much more accessible field vole found chiefly in fairly open grassland, where it is more readily captured in its runs.

The relatively small proportion of wood mice (*Apodemus sylvaticus*) in fox diet has recently been commented upon by Lockie (1957), who suggests that its deeper burrowing habits and ability to take flying jumps, render it a much more difficult animal for the fox to catch. Southern (1956), however, reported that, when rabbits were not available, foxes were digging into burrows of *Apodemus* in open spaces in pine woods.

From the skeletal remains and teeth of brown rats (*Rattus norvegicus*) recovered,

Table 2. *Instances of rodent teeth recovered from foxes*

	Number of foxes	Field vole	Bank vole	Water vole	Brown rat	Wood mouse	Total
STOMACHS: teeth present in 25%							
Aberdeenshire	6	–	–	–	–	–	–
Argyllshire	4	–	–	–	–	–	–
Cornwall	4	–	–	–	–	–	–
Derby	6	1	–	–	–	–	1
Essex	16	2	–	1	–	–	3
Flintshire	23	4	–	–	1	1	6
Hampshire	8	–	–	–	–	–	–
Kent	71	14	2	–	4	3	23
Westmorland	32	10	–	–	–	–	10
Total	170	31	2	1	5	4	43
SCATS: teeth present in 58%							
Berkshire	32	14	–	2	4	1	21
Cornwall	10	5	1	–	1	–	7
Hampshire	16	6	2	–	–	–	8
Kent	3	2	–	–	–	–	2
Westmorland	14	6	–	–	–	–	6
Total	75	33	3	2	5	1	44

it was seen that the bulk of this prey item was usually immature. Foxes often feed on house refuse or at garbage dumps in the country, in towns and in Service camps, so that the appearance of rats in the stomachs of foxes from urban areas is easily explained. However, as shown by Middleton (1954), rats are present in open country all the year round with considerable populations in hedges, field stone walls and old rabbit burrows, apart from farm buildings, corn ricks and such sites as sugar beet factories and root stores.

House mouse remains were identified only twice; no traces of harvest mice or dormice were found. The writer has been informed by Mr Harry V. Thompson that in Australia, where voles are absent, the house mouse is taken fairly often. Remains of small rodents occurred in nearly 60% of the stomachs and scats examined.

Remains of grey squirrels were found in only twelve foxes which had been shot in wooded areas of Kent (seven records) and Hampshire (three) with a single record

each from west Sussex and Berkshire. It is recognized that discarded bodies of squirrels, which were shot to qualify for the former 2s. tail bonus paid by the Forestry Commission, are likely sources of the remains found, and it is known that foxes can obtain access to squirrels caught inside various traps. Of the twelve records, seven were taken between the months of February and April. Since Shorten (1954) has shown that squirrels may have to travel far afield in order to get enough to eat during this period of food shortage, it is likely that many of these records represent animals caught foraging on the ground away from trees. Equal numbers of squirrel remains were found in male and female fox stomachs.

As would be expected, a marked difference occurs in the amount of sheep's wool present in the stomachs of foxes from lowland and upland areas. The presence of such wool often results from feeding on dead lambs, and this is confirmed by the occasional occurrence of calliphorid maggots inside fox stomachs. Much heavier losses are caused to lambs than to full-grown sheep and there is also a seasonal variation in the numbers of lambs killed. Stained wool from the crutch, thrown away after shearing, has been found in stomachs from Kent in the absence of any complaints of sheep losses. A bright yellow sample of wool was recovered in August 1957 from a Flintshire fox stomach; yellow sheep dip is used in this county between mid-June and the end of September.

Remains of deer were infrequent, being mostly roe deer from Westmorland. Pigs' bristles were more common, the animals presumably being taken by foxes as a result of too shallow burial after killing on the farm. In two cases, fragments of small hoofs coupled with blow-fly larvae suggested that such piglets had been eaten some time after death. Nine out of the ten pig remains were taken from stomachs of dog foxes. For convenience in tabulating, scarcer items from large animals are grouped together in Table 4 as carrion.

Dog hairs were rarely found and came mostly from Westmorland, Wales and Cornwall, where sheep remains were frequent. Two instances of hairs of Mustelidae, probably weasel, and one of cat were found. As might be expected, fox hairs occur fairly often, mainly in empty or nearly empty stomachs, doubtless from grooming of a fox's coat. Two immature fox teeth, claws and the typical grey, curly fur of a cub were found in a scat from a Berkshire wood, and may represent cannibalism by a larger fox.

Remains of hedgehogs were recorded five times; in one case from Cornwall only quills were found in scats, and in another from Kent the stomach contained hairs, with quills alone in the intestine. Only two instances of mole remains were found, the first in a $2\frac{1}{4}$ lb male cub from Kent, the second from a Berkshire scat found in March 1958. In the latter case, measurement of the straight portion of the lower jaw showed it to have come from an immature animal. Shrews were not found. Their glands are known to be strongly repellent to predators; if these animals are ever killed by foxes, they are very rarely eaten.

(*b*) *Birds*

Digestion of the whole or bulk of the vane of feathers frequently destroys the

barbs and barbules required for identification, the remaining rhachis or quill bases being virtually useless for this purpose. Understandably enough, foxes only rarely eat mouthfuls of primary feathers which would, if present, greatly have helped identification, and it therefore seemed best to group all gallinaceous bird remains as game and poultry. Compared with Southern & Watson's data (1941), there has been over twice the amount of poultry taken in the lowlands since myxomatosis (27·5 and 12%) but the percentage for the hills has remained the same (12·5 and 11·5%). As expected, the highest incidence of remains of game was found in foxes from the strictly preserved areas of western Kent. Pheasant feathers were more frequent than those of the common partridge, and in only one instance were identifiable remains found of a red-legged or French partridge. Grouse feathers occurred in three Westmorland foxes, and ptarmigan from two foxes from Argyllshire and Inverness-shire. Wounded and pricked birds would be included in the remains found.

Among the smaller birds, thrush, blackbird, starling, chaffinch and skylark were taken more than once. Rooks and crows (unseparated) and wood-pigeons were better represented; probably their bodies would often have been found dead by foxes after shooting so that all such records would not be true captures.

Isolated instances of moorhen, magpie, goose, duck and house sparrow remains were recorded; feathers of a herring gull found outside a Cornish earth were matched by similar feathers from a fox shot near the same site. In the lowland areas bird remains occurred in over 60% of stomachs, while in hill counties the figure dropped to 40%; this can be accounted for by the fewer birds and the more scanty cover available to the fox for stalking.

Egg shell or egg membranes, without any traces of accompanying feathers, have been noted both in stomachs and scats; the material takes the form of rather tough, buff-coloured membranes with a lamellate structure. Three samples examined by Dr C. Tyler of the University of Reading were regarded as probably from the domestic hen. Egg shell is known to be dissolved by the gastric juices after about 4 h in the stomach.

The only other vertebrate remains comprised the skin and bones of a young toad from the stomach of a fox shot in January 1956 on the moors of Westmorland. No scales of reptiles or fish were found in any of the material though both have been recorded occasionally by other workers.

(*c*) *Insects and other invertebrates*

Beetles provided the majority of the insects eaten by foxes, the Carabidae (ground beetles) and Scarabaeidae (dor beetles) being the two main families found. More remains of the former family occurred in wooded, lowland country and more of the latter in the Lake District, Wales and Cornwall. Fortunately, the commonest ground beetle, *Carabus violaceus* L., has smooth purple margins on the wing-cases, often enabling small fragments to be recognized. The next most abundant Carabid found was *C. problematicus* Hbst. *gallicus* Geh. while three more species (*C. arvensis* Hbst., *C. nemoralis* Müll. and *C. monilis* F.) were much scarcer. Other Carabids occasionally found were *Abax parallelopipedus* O. & M., *Harpalus*

rufipes Deg., *Pterostichus* spp. and *Pristonychus* spp. Two species of dor beetles, *Geotrupes stercorarius* L. and *G. spiniger* Marsh, occurred frequently in almost equal numbers while *G. stercorosus* (Scrib.), *Typhaeous typhoeus* (L.), *Melolontha melolontha* (L.) and *Aphodius rufipes* L. were rather infrequent. The appearance of the Australian spider beetle, *Ptinus tectus* Boiel., in the stomach of a fox from Kent was interesting. This flightless beetle, common in warehouses, has been shown by Woodroffe (1954) to occur in nests of pigeons and sometimes in those of house sparrows. The only other remains present in this particular fox were rabbit, rat and sheep's wool.

The only caterpillars found were those of the tussock-feeding dark arches (*Apamea monoglypha* Hnfn.) from Derbyshire and Herefordshire and the large yellow underwing (*Noctua pronuba* L.) from Cornwall.

Larval blowflies (*Calliphora erythrocephala* Meig.) occurred in stomachs containing wool and the writer has elsewhere described (Lever 1957) the occurrence in fox stomachs of large numbers of the larval Syrphid *Myiatropa florea* L. which is known to frequent water collected in hollows in beech and other trees.

Minor items found once were: earwig (*Forficula auricularia* L.), bibionid flies, eggs and larvae of undetermined Diptera, ant (no body) and the three weevils *Phytonomus arator* L., *P. punctatus* F. and *Alophus triguttatus* F. which are all about $\frac{1}{4}$ in. in length and were probably consumed with foliage. A solitary elaterid larva, *Athous* sp., occurred in the stomach of a Flintshire fox and remains of an adult *A. vittatus* F. from Cornwall; this county had the highest percentage of insects found.

Although a few insects were present between December and February (Table 6), most occurred between June and August, 26% in both the lowlands and the hills (Table 4). The frequency of occurrence of insect remains in fox stomachs seems to depend on the relative abundance of the insects in the field. It should be mentioned that Lancum's classification (1955) of insects as 'occasional' items appears rather low for British foxes and might better be raised to his category of 'common'.

The presence of chaetae of earthworms is easily overlooked, as these amber-coloured objects about 1 mm long sink with the grit to the bottom of the beaker with the fine material, which has passed through the $\frac{1}{25}$ in. wire sieve. Complete or nearly complete worms occurred in only two or three foxes. Although likely to provide only a small portion of the food of foxes, worms occur fairly frequently, often appearing in stomachs with voles as the only other remains. The frequency of worm remains was much lower in foxes from the moors of the Lake District and Scottish Highlands than in those from grassland and woods in the lowlands. Chaetae recovered from foxes sent from Kent were identified as from *Lumbricus terrestris* by Mr B. M. Gerard of Rothamsted Experimental Station.

Bodies of slugs are rapidly digested and were found only twice; small snail shells were also found twice.

(*d*) *Plant remains*

The only vegetable remains found in any quantity in fox stomachs were grass blades and culms; as pointed out by Scott & Klimstra (1955) it is difficult to

determine whether they were deliberately eaten or not. Owing to this problem in assessing such remains, plants are not listed in the tables with animals. The grasses identified at Kew were:

*Agrostis tenuis** (bent)
Agropyron repens (couch)
Brachypodium sylvaticum (slender false broom)
Cynosurus cristatus (dog's tail grass)
Dactylis glomerata (cocksfoot)
Festuca sp. near *pratensis* (meadow fescue)
*Holcus lanatus** (Yorkshire fog)
*H. mollis** (creeping soft grass)
Lolium perenne (perennial rye grass)
*Molinia caerulea** (purple moor grass)
Nardus stricta (mat grass)
Poa annua (annual meadow grass)

An asterisk denotes grasses which had been found growing by Summerhayes (1941) in two experimental areas in Roxburghshire and Merionethshire when studying plants associated with the field vole (*Microtus agrestis*). The presence of four species of grass both in the plots and in fox stomachs strongly suggests that some were obtained casually when catching voles in pasture. Summerhayes mentions *Molinia* and *Holcus mollis* as presumably forming the staple diet of voles in his two areas. Couch is known as a diuretic and emetic for dogs, and various grasses are likely to be taken deliberately as food by foxes.

Other remains found were leaves of cabbage, oak, maple, hawthorn, birch, walnut, juniper, yew, larch and pine. Herbs were represented by thistle (*Cirsium*), heather (*Calluna vulgaris*), dog's mercury (*Mercurialis perennis*), burnet saxifrage (*Poterium sanguisorba*) and white clover (*Trifolium repens*). Seeds of ash, leaves of cloudberry (*Rubus chamaemorus*) and bracken, three mosses (*Pleurozium*, *Hylocomium* and *Rhytidiadelphus*), the lichen *Cladonia* sp. near *impexa* and the pods of the meadow vetchling (*Lathyrus pratensis*). Fruits present were stones of sloe, plum and cherry, pips and skins of apples and pears and whole blackberries, mostly from foxes shot in the autumn; six fruit stones from December fox droppings from Cornwall suggested access to low-growing fruits of bullace (*Prunus institia*) observed at a nearby earth.

(e) *Miscellaneous items*

Various plant remains comprised such varied items as potato skins, straw, rotten wood, twigs and wood shavings. The following were also recovered: cinders, writing paper, newspaper and silver paper, string, a rubber band, cotton wool, pieces of cotton cloth, steamed bone (fertilizer), paraffin wax, bacon rind, and fat or lard. The last two items were from stomachs without the flesh or hair of large animals. One fox from Kent had remains of a large maxilliped and pieces of gills identified by Dr I. Gordon as being from an edible crab (*Cancer pagurus*), clearly suggestive of garbage feeding. A fox dropping from Berkshire contained an air gun or pistol slug which might have been fired into a pig's body, as portions of a hoof were also present, and pig bristles were recovered from other scats found nearby. Fragments of pottery, glass and pebbles were usually associated with game and poultry and no doubt came from their gizzards. Pieces of chalk and clay also occurred, and soil, sand and grit were commonly present in small amounts.

PRE-MYXOMATOSIS RECORDS

Only eleven stomachs from England and six from Scotland were obtained before the arrival of myxomatosis and, although a detailed comparison with the post-myxomatosis adult stomachs is therefore impossible, the items found from these seventeen individuals are tabulated in Table 3. In England, Lagomorpha are seen to have been over three times as numerous as rodents, a condition which was soon reversed when myxomatosis arrived. The high figure (64%) for remains of sheep in stomachs is largely due to most of these foxes having come from upland country. Similar results were obtained by Lever, Armour & Thompson (1957) when only ten pre-myxomatosis stomachs were available for examination.

THE FOOD OF THE ADULTS

Whereas the quantity of food found in the fox's stomach obviously depends on the period elapsing between the previous meals and death, the writer has been informed by Dr J. Valverde of Almeria, Spain, that post-mortem digestion is frequent in the Carnivora. As periods up to 4 days sometimes elapsed between the

Table 3. *Food items from fox stomachs taken in the pre-myxomatosis period*

		Numbers of stomachs	Rabbit and hare	Rodents	Sheep	Deer	Birds	Insects
Westmorland	March-May 1955	8	4	1	5	2	2	4
Cheshire	March 1955	1	1	–	–	–	–	1
Derbyshire	March-April 1955	2	2	1	1	–	1	–
Argyll	May 1955	6	1	1	5	–	2	3
Totals		17	8	3	11	2	5	8

killing of an animal and its arrival in the laboratory, this post-mortem digestion is likely to have been fairly usual. With one exception, the stomach contents had an air-dry weight ranging from < 5 g to 150 g, the average being 25 g. The one heavy stomach weighed 300 g (dry) and came from a dog fox known to have been shot soon after robbing a hen roost. Hoffman & Kirkpatrick (1954) weighed the stomach contents of thirteen red foxes (*Vulpes fulva*) finding an average weight of 102 g; they do not, however, state whether their material was weighed dry or wet. Small-scale feeding tests, carried out at the premises of the Zoological Society of London, were made with the co-operation of Mr Oliver Jones, M.R.C.V.S. For each test an albino rat was given as food after the fox had been on a rodent-free diet for 1 week. The droppings, collected periodically, were then examined for hair and bones. It was found that the bulk of the food was passed within 48 h of feeding Approximately one-quarter of all stomachs from adult wild foxes proved to be empty or nearly so: England 25% (72/290), Scotland 20% (6/29) and Wales 24·5% (16/65). Southern & Watson (1941) similarly found 21·5% (11/51) of the stomachs they examined were empty. A similar proportion

was also found in Finland by Lampio (1953) who, however, recorded more empty male than female stomachs; this was not confirmed for Britain. Cobnut reported (1955) that during the spring of that year 'by far the greater number of over 100 stomachs' from Kent were empty.

In Table 4 the items found in 372 lowland foxes are compared with those from 106 hill animals. Lowland and foothills are usually situated below 600 ft and hills are from 1000-2000 ft altitude. It will be seen that there is little variation between the total Lagomorpha (24·5% and 34%) and small rodents (59% and 58·5%) recovered from these two main areas but much difference between sheep (9% in the lowlands and 33% in the hills) as well as birds (63% and 40% respectively).

Four counties (Kent, Westmorland, Flintshire and Berkshire) provided more than forty-five specimens each and the data for these 225 foxes are given in Fig. 1 in the form of histograms. The extremes are the Kentish woodlands and the moors of the Lake District, while the foothills and farmlands of Flintshire and

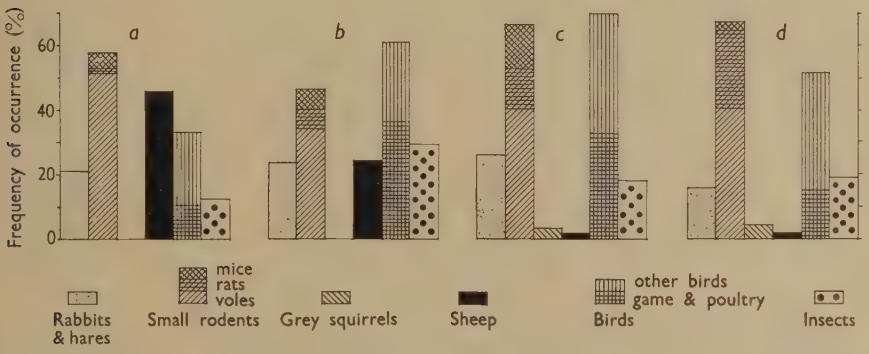

Fig. 1. Food items from 225 fox specimens: *a*, Westmorland (66); *b*, Flintshire (55); *c*, Chevening Park, Kent (56); *d*, Berkshire (48).

grassland with mixed woods of Berkshire are intermediate both in topography and food categories. This last locality was represented by remains from scats collected and documented by Mr R. M. Newson of the Bureau of Animal Population, Oxford.

Data from the Chevening Park area, derived from thirty-one foxes shot in 1955-6, when compared with twenty-five from 1957 showed a twofold increase in the rabbits and hares taken after the acute phase of myxomatosis (Table 5). Small rodents occurred in some 65% of the stomachs and scats but sheep remains accounted for only 3%. This area of undulating mixed pasture with adjoining woods of oak, beech and ash has also a number of poultry farms, piggeries and cornstacks, which form ideal territory for providing prey for foxes. The items recovered from foxes shot in the nearby Penshurst Park agree well with those from Chevening Park which has less extensive areas of coniferous trees. Feathers of game birds were frequently found in fox stomachs from this strictly preserved

Table 4. *Post-myxomatosis records of food (% frequency of occurrence) of 478 adult foxes*

This table excludes seventeen pre-myxomatosis records given in Table 3 and thirteen empty stomachs.

		Specimens			Rabbit and hare	Small rodents				Grey squirrel	Carrion§ Sheep & deer		Hedge-hog	Game and poultry	Total birds	Insects¶
		Stomachs	Scats	Total		Voles†	Rat	Mice‡	Total							
LOWLANDS																
Beds. (2) Lincs. (1) Bucks. (2) Middx. (3) Cheshire (1) N'hants.(3) Derby (10) Notts. (8) Essex (23) Oxon (2) Herts. (1)	Jan. 1955-Aug. 1957	54	2	56	30	46·5	9	3·5	59	0	3·5	5	0	39	64	28·5
Berkshire	Nov. 1957-Apr. 1958	0	48	48	14·5	43·5	23	2	68·5	4	2	8	2	14·5	52	18·5
Western Kent: Chevening Park estate	Mar. 1955-Nov. 1957	55	1	56	27	41	12·5	12·5	66	3·5	1·5	5	0	32	70	18
Penshurst Park estate*	Feb. 1955-Nov. 1957	55	3	58	31	38	8·5	12	58·5	8·5	3·5	1·5	1·5	38	62	13·5
Hants. (32) Surrey (5) Mid-Kent (8) Sussex (7)	Mar. 1955-Jan. 1958	32	20	52	32·5	38·5	13·5	9·5	61·5	7·5	0	2	0	23	63·5	25
Cornwall (25)* Pemb. (3) Glos. (4) S'set. (2) Herefs. (7)	Mar. 1955-Apr. 1958	23	18	41	39	53·5	5	5	63·5	0	22	5	2·5	22	50	63·5
Denbigh (2) Flint (53)	Nov. 1956-Dec. 1957	52	3	55	23·5	34·5	5·5	5·5	45·5	0	23·5	5·5	2	36	60	29
Fife (4) Kinross (2)	Apr. 1955-Aug. 1956	6	0	6	0	33·5	16·5	0	50	0	16·5	0	0	16·5	83	16·5
Totals and averages		277	95	372	24·5	41·5	11·5	6	59	3	9	4	1	27·5	63	26·5
HILLS																
Westmorland	July 1955-Feb. 1958	52	14	66	21	51·5	1·5	4·5	57·5	0	45	4·5	0	10·5	33·5	12
Brecon (5) M'gomery (5)	May 1955-Nov. 1957	9	1	10	0	70	10	0	80	0	20	0	10	0	20	10
Aberdeenshire	Apr. 1955-July 1957	12	0	12	58	33	8·5	0	41·5	0	33	0	0	25	66	25
Argyll	Feb. 1956-June 1957	5	0	5	0	80	0	0	80	0	60	0	0	20	40	60
Banff (8) Inverness (5)	Apr. 1956-Apr. 1958	0	13	13	92	23	7·5	0	30	0	7·5	7·5	0	7·5	38	23
Totals and averages		78	28	106	34	51·5	5·5	1	58	0	33	2·5	2	12·5	40	26

* *Mus musculus*, Penshurst Park and Cornwall. † Chiefly *Microtus*. ‡ *Apodemus* unless otherwise recorded. § Non-sheep carrion. ¶ Excluding larval Calliphoridae.

Table 5. *Food eaten (% frequency of occurrence) by 180 foxes in 1955-6 and 1957*

		Number of stomachs	Rabbit and hare	Small rodents				Grey squirrel	Sheep	Carrion and deer	Hedge-hog	Game and poultry	Total birds	Insects*
				Voles	Rat	Mice	Total							
Chevening Park estate, west Kent	Mar. 1955-Dec. 1956	31	19	42	13	13	68	6·5	3	6·5	0	35·5	61	16
	Jan.-Nov. 1957	25	36	40	12	12	64	0	0	4	0	28	80	20
Penshurst Park estate, west Kent	Feb. 1955-Dec. 1956	35	20	40	8·5	14·5	63	6	3	0	3	34	63	8·5
	Jan.-Nov. 1957	23	48	34	9	9	52	13	4	4	0	43·5	60	22
Westmorland (mostly Langdale and Mardale)	July 1955-June 1956	25	28	40	0	4	44	0	52	4	0	12	44	16
	Sept. 1956-Feb. 1958	41	17	58·5	2·5	5	66	0	41·5	5	0	10	27	10

* Excluding larval Calliphoridae.

locality. In contrast to Kent, the Westmorland records of lagomorphs are much reduced in the later period (1957) and the small rodents are correspondingly increased from 44% to 66%. Many of the foxes were shot on upland moors at altitudes of 1000 to 2000 ft near Langdale, Longsleddale and Shap. Coarse tufted grass and bracken predominates, and the area was known to have many voles during 1957, thus accounting for two-thirds of the fox stomachs with rodent remains. Sheep, some known to be carrion, occurred in more than 45% of the stomachs. It is, of course, appreciated that 'hill' foxes move down into the valleys to feed on poultry and may be shot there. The amount of game and poultry taken (18%) was about one-third of that from Kent.

An attempt was made to assess the relative proportions of the different food items from one area over a period of 12 months. Table 6 shows such records from sixty-five fox stomachs from western Kent which was the only locality in which enough specimens were taken within any 12 months for such detailed treatment. In autumn, rodents formed 75% of the diet and birds 66%; the former group remained nearly as high during the winter when birds dropped to about 40% with

Table 6. *Seasonal variation in kinds of food (% frequency of occurrence) in sixty-five fox stomachs from western Kent, September 1956-August 1957*

	Number of stomachs	Rabbit and hare	Small rodents	Grey squirrel	Game and poultry	All birds	Insects*
September-November	12	25	75	8·5	50	66	16·5
December-February	19	26	73·5	10·5	21	42	16
March-May	23	43·5	56·5	9	30	69·5	17·5
June-August	11	36	36	–	18	82	36

* Excluding larval Calliphoridae.

insects at 16%. During the spring, both grown and nestling birds are abundant and this item reached nearly 70%. Unfortunately the number of stomachs available throughout the summer was only eleven: birds then reached over 80%, rodents were at their lowest (36%) and insects at their highest (36%). These relative proportions are in accord with American and Finnish figures.

THE DIET OF CUBS

As cubs can exercise little selection in the choice of food, the contents of their stomachs were given separately from freely ranging adults. Only thirty-five cubs' stomachs were available, twenty-five from Kent, four from three other English counties and six from two Scottish ones. A cub was defined as an animal weighing not more than 5 lb and was usually about 3 months old. The percentage frequency of occurrence of items found in the stomachs of the Kentish cubs were: birds 60%; lagomorphs 25%; small rodents 20%; grey squirrels and moles 4% each. The high figure for birds is easily accounted for as all the English cubs were sent in while nesting was at its height. Of the two moles found in over 500 stomachs and scats examined, one came from a cub, a male of 2¼ lb.

DISCUSSION

Comparison of the items of diet found in 1955-7, based on 478 specimens, and those recorded by Southern & Watson (1941) in 1939-40 (fifty-eight specimens) shows some major differences, largely due to the effects of myxomatosis which arrived after September 1953. In the data set out in Table 7, most of the pre-war hill foxes came from Wales, whereas the later ones of this survey were chiefly from the Lake District. The item 'Other birds' for 1939-40 is derived from the total of large and small birds excluding poultry, whereas for 1955-7 it represents remains of all birds except game and poultry. The outstanding differences over the two periods between the relative amounts of lagomorphs, voles and poultry in the lowlands contrast with the general agreement between sheep, poultry and other birds and remains recorded in the hills.

For Scotland, the present results are comparable with those obtained by Lockie (1956) whose examination of ninety-eight fox droppings and fourteen stomachs showed that voles, hares and rabbits formed a large part of the diet of upland

Table 7. *The food of foxes before and after myxomatosis* (% *frequency of occurrence*)

	Lowlands		Hills	
	1939-40	1955-7	1939-40	1955-7
Sheep	4	9	38·4	33
Lagomorpha	68	24·5	48·5	34
Voles	4	41·5	15·4	51·5
Poultry and game	12	27·5	11·6	12·5
Other birds	28	35·5	25·4	27·5
Insects	20	26·5	11·6	26

foxes. Watson (1955) indicated that ptarmigan, hare, red deer and rabbit were represented in six highland foxes from Aberdeenshire.

There is a paucity of detailed field information in Britain on the relative proportions in which different categories of prey appear in the fox's diet. Sanders (1943) lists only the stoat and weasel, but not the more important fox, as mammalian predators of field and bank voles. However, in a field study by Middleton (1954) showing the toll that various predators exert on partridges in a small keepered area in Hampshire, foxes were found to be second in importance to rooks and crows, causing a 19% (54/284) loss of nests. Cobnut (1955) states that more than thirty sitting hen pheasants and a few early partridges were taken by the parent foxes for a litter of seven cubs in Kent between late April and mid-May. Cadman (1957) shows that during the winter of 1956 and early spring of 1957, foxes in North Wales fed mainly on voles, as confirmed for Flintshire by analysis of fox stomachs (Table 4). Scott's detailed work (1943) on American foxes, which entailed field observations as well as their food patterns, may be compared with the seasonal diet for 1 year in Kent as given in Table 6. Lampio's data from Finland (1953) reveal similar seasonal variations in a very different environment. In a later paper, Scott & Klimstra (1955) show that although American meadow

mice (*Microtus*) were only about one-fifth as numerous in the field as *Peromyscus* (corresponding to *Apodemus* in Britain) yet the former rodent was, as shown by its remains, much the preferred food of the red fox. Remains of carabid and scarabaeid beetles were, as in the writer's experience, of about equal frequency and were by far the most frequently eaten insects. The question of what is the food chosen by the fox can be briefly answered by saying that availability plays a major part in determining the items eaten. Thus when myxomatosis had reduced the rabbit to the status of a rare animal, the fox immediately switched to small rodents, chiefly field voles; records showed no noticeable reduction in its weight, condition and breeding. Thompson (1956) wrote that foxes were eating whatever was available and this is confirmed in the wide range of food items recovered during the present survey.

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SUMMARY

1. Analyses are given of the items found in 420 stomachs and 123 droppings (scats) of foxes collected mainly between February 1955 and August 1957. Most material came from south-east England; Kent accounted for over 40% of the English foxes. About one-quarter of the stomachs were quite or almost empty.

2. The commonest prey item was the field vole (*Microtus agrestis*) which has largely replaced the rabbit after the advent of myxomatosis. Voles were found in over 40% of stomachs from the lowlands and in 55% from the hills. The brown rat (*Rattus norvegicus*) was the next most commonly found rodent.

3. Owing to myxomatosis, rabbit and hare remains in 1955-6 occurred in only about 20% of fox stomachs in southern England compared with about 50% in 1939-40.

4. In the lowlands sheep's wool occurred in only 9% of the specimens compared with 33% from the hills, some of this being known to be from carrion. The capture of small rodents from both areas was similar (59% and 58% respectively).

5. Birds featured much more (63%) in the plains than in the hills (40%); game and poultry remains represented from one-half to one-third of all birds eaten. Pheasant and partridge were especially important items in preserved areas in western Kent.

6. Grass was the most abundant vegetable item, much of it probably swallowed casually by the fox when capturing small rodents. An extensive selection of other plant remains and of miscellaneous items was recovered. The wide range of all food categories shows the fox has a very catholic taste and takes whatever food is readily available.

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A SIMPLE PORTABLE RECORDER FOR DIRECTION AND SPEED OF WIND

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(With 3 Figures in the Text)

Continuous records of wind speed and direction in local situations would frequently be of use in the study of insect distribution and dispersal. There appears to be no instrument already available which will produce such records cheaply. The recording unit described has given results of sufficient accuracy to be useful to the field ecologist. The sensing element for wind speed is a modified portable Sheppard cup anemometer, and for direction a wind vane (not illustrated) consisting of a counterbalanced laminated plastic vane on an 18 in. wooden arm attached to the top of a steel spindle. Records are obtained in the form of inked traces on two charts which are changed daily. The details of the apparatus are shown in elevation and plan in Fig. 1.

The modification to the anemometer consists in fitting to the dial pointer a fine platinum wire which makes electrical connection with an insulated platinum contact once during each revolution of the pointer. Leads from the fixed, insulated, contact and from the (earthed) pointer contact pass to a miniature electromagnet (Fig. 1) and a battery in the recorder casing. The electromagnet causes an armature attached to the wind speed pen arm to be deflected, producing a mark on a drum chart. As the chart is rotated by clockwork, successive marks are recorded, their frequency (= distance apart) being proportional to the wind speed. In high winds the marks are so frequent as to necessitate a considerable chart speed, of the order of 10 in./h, and this is achieved by causing the pen carriage to move slowly and steadily parallel to the long axis of the drum, which rotates once per hour. In this way a spiral trace is obtained, of total length about 20 ft, on a chart which measures about 5×10 in. Such a chart is shown in Fig. 2.

The wind speed chart drum is removed by raising it until the contrate gear at the lower end of its spindle is disengaged from the driving gear, tilting slightly and lowering it to free the top end of the spindle from its journal bearing; it is replaced by an alternative assembly with a fresh chart.

Wind direction is recorded on a second, narrow drum attached directly to the wind vane spindle and rotating with it. The pen which traces on the direction chart is also moved steadily along parallel to the drum axis. Changes in direction of wind result in the pen trace travelling round the chart and vertical lines can be drawn on the chart, at intervals of one-quarter of its circumference, representing the cardinal points. A specimen chart is shown in Fig. 2*b*. Since there must be one compass direction which will result in the pen traversing the join in the chart

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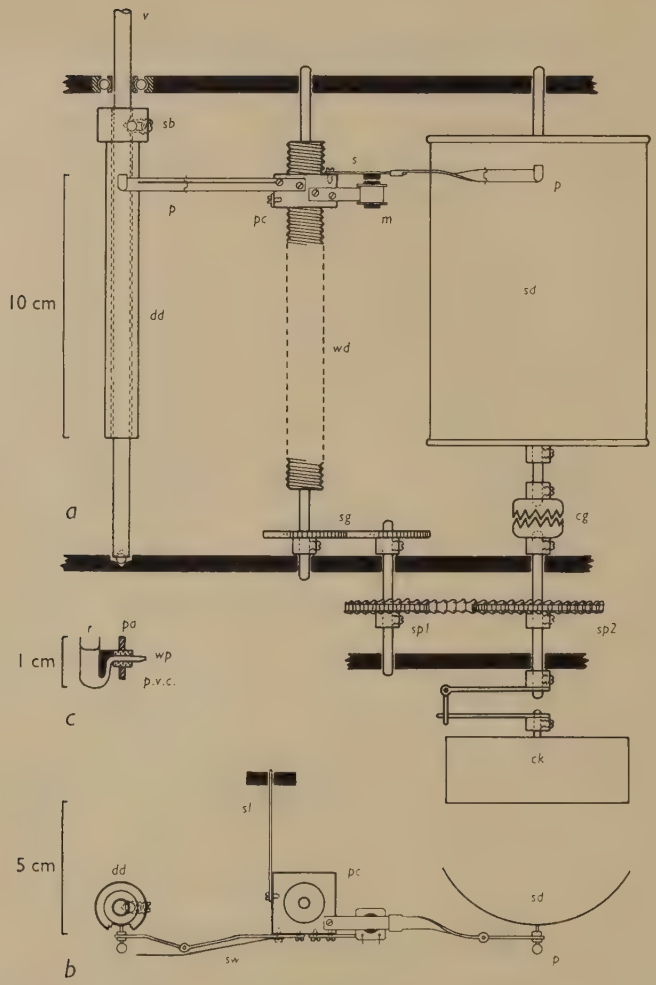

Fig. 1. Drawings, approximately to scale, of the recorder: *a*, elevation; *b*, plan; *c*, detail of glass instrument pen.

v, spindle of wind vane
sb, spring-loaded ball locating drum
p, glass pen
pc, pen carriage
dd, direction drum
s, spring
m, electromagnet
wd, worm drive to pen carriage
*sp*1, *sp*2, sprockets, 1 in. and 2 in. diameter respectively
cg, contrate gears, $\frac{3}{4}$ in. diameter, serving as coupling
sd, wind speed drum
ck, clock, drive taken from minute spindle
sl, sliding locator
sw, safety wire
r, reservoir
pa, pen arm
wp, writing point
p.v.c., polyvinylchloride bush
sg, spur gears, 48 teeth

it is important to use thin paper and to stick it down well along its length. Even so, the pen may be flirted from the chart occasionally whilst traversing the join, but is immediately returned as it hits the stiff safety wire attached to the carriage

(Fig. 1*b*). In practice it is found that the glazed chart paper supplied in rolls for commercial electrical chart recorders is satisfactory, and a latex formulation applied by a proprietary 'glue pen' is the simplest fixative. For convenience in interpreting the record, the wind direction drum is located in a standard manner by means of a sprung ball locating in a conical depression in the spindle. The drum is slid off the lower end of the spindle, the latter being raised from outside the casing, and an alternative drum with a fresh chart replaced. If the join in the chart paper is always positioned beneath the pen when the vane is in the same position, it is unnecessary to remember to mark the direction on the chart each time it is fitted. Charts are removed by slitting with a razor blade.

The translatory movement of the pens is obtained by mounting them on a carriage which travels down a worm when the latter is rotated by the clock. A countershaft carrying a spur gear and a chain sprocket is interposed to reverse the direction of movement of the clock so that the pen carriage travels down the

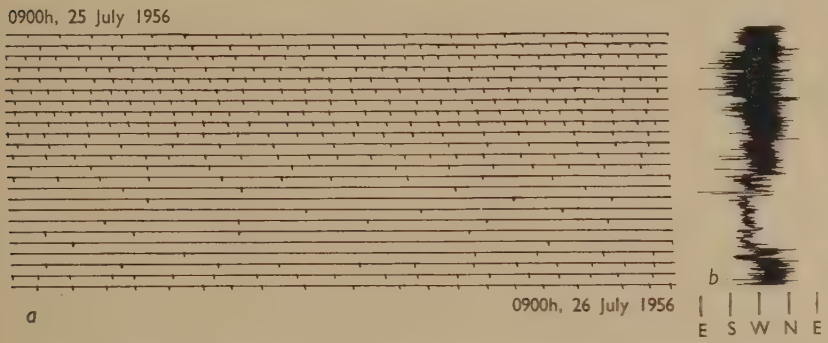

Fig. 2. Specimen records from the recorder: *a*, wind speed chart; *b*, direction chart.

right-hand threaded worm with time. The forked coupling between the clock spindle and the rest of the mechanism is hinged so that it can be disengaged when the charts are changed and the pen carriage reset to the top of its travel by manually counter rotating the worm. Rotation of the pen carriage on its axis is prevented by a sliding stop, shown in the plan view. It is convenient to hinge this stop so that it may be disengaged, allowing the carriage and pen arms to rotate a quarter turn, facilitating access to the drums when changing charts.

The clock is a cheap 5-in. alarm clock fitted with a slightly stronger mainspring than is standard. The electromagnet is from a Siemens high-speed relay and is driven by a 3-volt dry battery in series with the anemometer contacts.

Calibration of the modified anemometer in the wind tunnel showed no perceptible variation from the unaltered state. Fig. 3 shows a calibration for low wind speeds, which can be considerably extended if necessary. Spot readings of wind speed are easily obtained by measurement of the interval between successive marks on the chart, and mean winds by counting the number of marks during the

chosen time. The appearance of the chart (Fig. 2*a*) shows at a glance periods of calm, light or strong winds or gustiness.

Mention must be made of the pens themselves which are of novel construction (Fig. 1*c*). They are quickly made from soft glass using a bunsen burner, and are more reliable than the conventional trough nib, requiring much less frequent filling and giving an even trace in all directions with less sticking. The U-bend serves to trap dust which might otherwise clog the capillary. The nibs are sealing-waxed into short lengths of P.V.C. insulation taken from electric wire and this is pushed into holes drilled in the light aluminium pen arms. Such nibs have been in use for

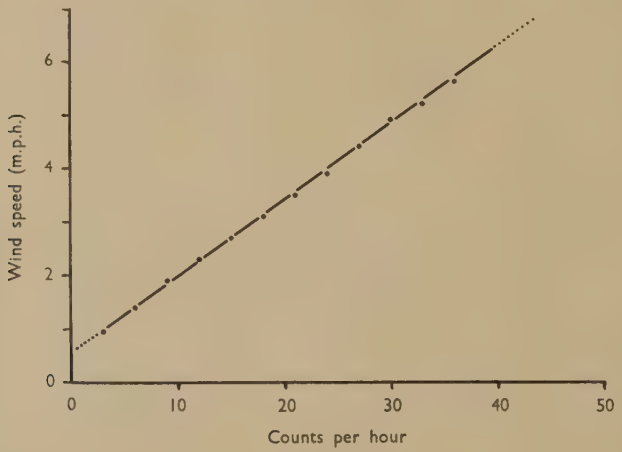

Fig. 3. Calibration curve of the modified Sheppard cup anemometer. (This calibration covers only the lower wind speeds: the range of the instrument is considerably higher.)

over 8 years at the Imperial College Field Station on conventional barographs, thermographs and hygrographs.

It is noteworthy that the part of the apparatus recording wind speed is suitable for recording any variable expressed in terms of pulses spaced in time. It has, for example, been used in this department for recording the passage of ants past a photoelectric cell: other uses will suggest themselves.

The whole recorder (less the anemometer and wind vane itself) fits into a waterproofed box about $12 \times 12 \times 6$ in., and the cost of materials, apart from the Sheppard anemometer, is less than £5. Meccano gears, sprockets and spindles are used, and the anemometer, but not the wind vane, can be at any distance from the recorder.

REVIEWS

GAME IN RUSSIA

A Survey of Russian Game Report Translations: Vols. 1-2 (1957) and 3-4 (1958). Ottawa: Queen's Printer. Price $1.00 per volume.

The articles translated in the first three of these octavo volumes originally appeared, in recent years, in the Russian annual publication *Biology of Furbearers* issued by VNIO, the All-Union Scientific Research Institute of the Hunting Industry under the USSR Ministry of Supply. A resolution of the 1956 Canadian Federal-Provincial Wildlife Conference, held at Vancouver, recommended that the Canadian Wildlife Service should arrange for translation of such articles, and for their distribution to game administrators in Canada. The reason for this recommendation is fairly obvious, since the mammals discussed—beaver, muskrat, and arctic and red fox—are all represented by the same or closely allied forms in the fauna of North America. Much of the data on the habits, life histories, parasites and economic aspects of these species in Russia is thus likely to be useful also to those concerned with game management in Canada. The translations have been done by Dr J. M. MacLennan, until recently of the Canadian Wildlife Service, who has during the past 2 years kindly supplied copies to the present writer as they were issued. No account of them seems to have appeared in this country, and their interest is such as to make some account of them desirable here.

Volume 1, on the beaver, contains 109 pages comprising translations of papers by seven authors, published from 1951 to 1955 inclusive (like the papers in volumes 2 and 3), in the journal *Biology of Furbearers*. Three of the papers deal with re-acclimatization of beavers in areas where they had been completely, or practically, extinct for a considerable time—in Archangel Province, in the Ob River basin, and in the Tatar ASSR. From twenty-six beavers released in the course of 13 years in the Kholmogorsk district of Archangel, the resulting beaver population in 1951 was estimated at 250-300; but it was thought that it would be a long time before their numbers would become large enough for economic trapping, unless introduction was carried out on a much bigger scale. In addition to fresh introductions, various measures for improving local ecological conditions for the beavers are recommended, and it is believed that there are great possibilities for creating a beaver population of high numbers and density. In the Ob River basin experiments the beaver population is estimated to have increased fivefold in 7 years, and to have spread some 500 km from the place of release. There are considered to be many places in this region suitable for beaver habitats, which should be colonized by these valuable fur-bearers. The animals have apparently established themselves also in the Tatar ASSR, but a considerable part of the valley where colonies are found will be submerged owing to the rise in the water level caused by the construction of a power station at Kuibyshev, and it may be necessary to remove the beavers to new locations.

Other papers in this volume deal with the biology of beavers in winter in the Province of Archangel, their present distribution in the Ukraine (where they have been much reduced), the experimental planting of willows, considered to be the most important of all trees as beaver food, and experimental treatment of helminth infestations in beavers with a mixture of chenopodin and castor oils followed by phenothiazine.

Volume 2 runs to 224 pages of translation of eleven papers on the muskrat. The titles of some of them indicate the practical and economic outlook which motivates these papers throughout, e.g. 'Better Ways of Trapping Muskrats', and 'Raising "Black" Muskrats', while again several deal with acclimatization; but in them all there is much material of biological interest. One paper on internal and external parasites of muskrats

discusses the results of examination of 813 specimens, of which 56.8% were found to be free from helminths and 43.2% with some degree of infestation. Ten species in all of parasitic worms were found. A distinct geographical correlation was noted, the northern provinces having a higher number of infested muskrats than the central and southern districts. The muskrat, now widely distributed over northern Russia and Siberia as well as in several southern regions, is the only animal discussed in this series of volumes which is not indigenous to the USSR, but has been introduced in recent times from Canada and from Finland and England. Comparison of all the published data on parasitic worm infestation of muskrats, in their previous range, with the infestation of the stock now established in Russia indicates that sixteen species of helminths have been recently acquired. The final paper discusses fluctuations and forecasts of muskrat numbers, and states that 'Study of the results of acclimatization of muskrats ... and statistics of muskrat fur production show an absence of definite periodicity in fluctuations in numbers ... Several foreign scientists, such as Elton and Nicholson, see in the fluctuations in numbers of muskrats an automatic feature, and try to prove the existence of a definite, unvarying periodicity, although the factual material presented by them does not accord with their assertions'. The actual words of these authors, in concluding their paper in Volume 11 of the *Journal of Animal Ecology*, were that the investigation 'shows that there has been, since about 1850 at any rate, a strongly marked cycle in numbers of muskrats with an average period of recurrence of about 10 years'. Although the original Russian paper was published as lately as 1955, the bibliography does not include, as one might have expected, any of Errington's papers on muskrat fluctuations in the United States.

Arctic and red foxes are the species discussed in the ten papers in Volume 3 (214 pp). In an account of 'Dynamics of Fox Numbers in Voronezh Province and Forecasting of Fox Harvests' (by one of the two women biologists who are responsible for five of the papers), a graph illustrates a noticeable correlation between the estimated population of foxes and that of small mouse-like rodents over the period 1944-50. A detailed account of the helminths of red foxes in the Tatar ASSR, a subject on which very little was previously known, revealed that, over several years of study, the foxes were 100% infested with parasitic worms, which included three species of trematodes, eight of cestodes, seven of nematodes and one of acanthocephala. Nematodes were the most widely distributed, occurring in 88.5% of the animals examined. The extent and intensity of infestation varied according to season (foxes taken in December and January were the most heavily parasitized) and locality (higher in zones with a varied than in those with a uniform topography). Ectoparasites also come in for discussion, in two papers on 'Mange in Wild Foxes' and 'Mass Diseases of Foxes in the Crimea'. Four of the papers deal specifically with arctic foxes, and two others describe techniques of catching and tagging fox-cubs.

The volumes are free from any political polemics such as obtrude occasionally, for example, in the English version of I. Khalifman's book on the honey-bee, and contain much information which should be of considerable interest to zoologists generally, as well as of assistance to game administrators in Canada. One criticism that may be made, applicable to the originals and therefore not to the translations, is that the papers in many cases give only the Russian names of the animals mentioned in their titles, and not the scientific ones. Sometimes this may be of little consequence—there is only one species of beaver in Europe (though even in this case two subspecies, according to Ellermann and Morrison-Scott's *Checklist of Palaearctic Mammals*, are found in Russia or adjacent parts of western Siberia). Within the same area several subspecies of the red fox, *Vulpes vulpes*, are stated to occur; but only one of the authors in the volume on foxes specifies the two subspecies he is dealing with, and these from his account appear to differ to some extent in habits as well as in physical characters.

There is seldom any reference to research done in other countries; out of sixty-one books or papers listed in the bibliographies in the fox volume, the only non-Russian item is a composite reference to the results of the Canadian Arctic Wildlife inquiry published in this Journal in the years between 1937 and 1950. In view of the attention given in some of these papers to the fluctuations in the numbers of small rodents on which the foxes largely feed, it is rather surprising to find no mention of Elton's *Voles, Mice and Lemmings*.

Volume 4 of the series (159 pp.), recently issued, breaks new ground in two respects: in being the first to deal with birds, and also the first to constitute a translation of a complete book (by S. M. Uspenski, published in Moscow in 1956). Entitled 'The Bird Bazaars of Novaya Zemlya', it gives a vivid picture of the immense numbers of birds found in the season at the colonial nesting-places (called locally 'bazaars') of species of Alcidae, gulls and various other sea-birds occupying a considerable part of the steep rocky coasts of that island. 'Like bees in front of a gigantic hive, innumerable flocks of birds swarm about the steep coastal cliffs. In places the natural colour of the cliffs is invisible under the coating of dried bird-droppings and the multitude of birds that occupy every projection, crevice, and ledge. A careless shot near by loosens from the cliffs an avalanche of birds capable of upsetting a boat lying in the water and of throwing its amazed occupants into the sea.'

The species chiefly found in these vast assemblages are Brünnich's guillemots, kittiwakes, black and common guillemots, glaucous gulls, puffins and 'dovekies' (little auks); Brünnich's guillemot being by far the most numerous and the most important economically. A table giving approximate estimates of the numbers of Brünnich's guillemots and kittiwakes at the forty-seven Novaya Zemlya 'bazaars' records totals of at least 1 883 000 of the former and 30 400 of the latter. This is followed by a chapter on Brünnich's guillemot and another on the six other species mentioned; food, habits, seasonal movements, growth, reproduction and eggs, predators and endoparasites, and interrelations with the other birds being discussed under each species.

The final chapter deals with the economic utilization of the bazaars in the past and today, and with prospects for the future. The bazaars produce fresh eggs and meat, especially valuable in the far north where it is difficult to provide the people with fresh vitamin-containing foods. Eggs, meat and skins of Brünnich's guillemots are also exported to other parts of Russia, and also to a smaller extent the eggs of the common guillemot and the kittiwake. From 1930 to 1950 the total number of eggs exported was, from the (incomplete) data available, about 3 000 000, and the number of birds, 500 000. The purpose of the whole work is indicated in the statement that 'Expanded production—an essential feature of Socialist economy—calls for only such economic use of bird bazaars as will permit concurrent increase in their bird populations.' Various measures towards that end are discussed, and as an example of the need for them it is mentioned that in 1933 the largest *murre* (guillemot) nesting colony was almost completely wiped out by the taking of 342 500 eggs and over 12 000 of the birds themselves.

The volumes are well produced, by a very effective duplicating process, on good paper, and with printed stiff red paper covers. The translations read easily and naturally, and the Canadian Wildlife Service and Dr MacLennan are to be congratulated on making this series of studies available to English-speaking biologists. They are obtainable from the Queen's Printer, Ottawa, at $1 per copy.

There are many things one would wish to know about the Russian researches and experiments, present and past, on wild animals as sources of food and fur; the subsequent fate, for example, of the immense rabbit-farms established in the nineteen-thirties by G. A. Philippoff in various parts of the USSR to provide meat in the absence or depletion of normal flocks and herds. It is to be hoped that another translator will continue the work so well begun.

COLIN MATHESON

ECOLOGICAL TEXTS

E. P. Odum (1959). *Fundamentals of Ecology.* Second Edition. Pp. xvii+546; 1 plate; 160 text-figures and photographs. Philadelphia and London: Saunders. Price 52*s.* 6*d.*

It is becoming increasingly clear that, if the human species is to continue, the ideas of ecology must be more widely understood and applied. Those who believe this to be so and who try to teach ecology to potential ecological technicians are faced with many problems of selection and presentation in a subject notorious for its diffuseness and its high ratio of observation to principles. The reduction of ecology to an assimilable teaching subject involves the choice of material at three distinct levels, namely the range of topics to be covered, the amount of subject matter to be included under each topic, and the diversity of views to be presented on each point.

Recent reviews of ecology textbooks have contained much caustic comment but little agreement on the range of topics which the authors should have included within ecology. Odum's book covers practically all those topics about which papers are currently written in those journals whose titles include the word. In addition there is a useful section based on his personal experiences of radiation ecology, a subject which ecologists must certainly master from now onwards. The book is very logically arranged and the use of a standard presentation involving a definition, followed by explanation and examples results in an ample amount of fact to balance the general ideas. Inevitably there is variation in the profundity of the different parts; the section on energetics and productivity will be welcomed by anyone familiar with this field and is an important résumé of new work; this would be distinctly hard going in places for the novice; the population dynamics section, on the other hand, is much more superficial.

There is a tendency, both in teaching and in organizing one's own thoughts on a rapidly growing subject, to use a historical framework and to accumulate successive ideas which are labelled after their supposed originators. Such a method may ensure that rough justice is done to the contributors to a science and that, when a phrase or term is used, we appreciate its limitations and precise meaning. As a basis for planning a textbook, however, the historical approach may conceal a reluctance to face reorganizing the facts and ideas and may burden the student with much that is irrelevant to an understanding of the principles of the subject. He is left in no doubt about Professor Odum's use of terms, but the question which troubles your reviewer is whether the student will appreciate that many of these definitions conceal a morass of controversy and even that some of them are not those in general use.

Odum is perfectly frank about his attitude to definitions; he states that 'words which are not only widely used in science but in general language as well should be precisely defined but should remain broad in scope. It is much less confusing for everyone to leave the basic term broad, and then "subclassify" by means of adjectives or modifying phrases where a more restrictive meaning is in order'. His use of such terms does, on the whole, approximate closely to their everyday meanings and the result would be wholly admirable if only the student were warned that, owing to the perverse accidents of the history of science, many terms have acquired special scientific meanings and are not used in this everyday sense by the majority of ecologists. Thus the term 'assimilation' is an obvious one to use for the total intake of energy and matter into an organism or a trophic level; unfortunately, however, the majority of workers in this field on both sides of the Atlantic happen to use the word 'production' in this sense. Odum's common-sense use of the expressions 'density dependant' and 'competition' only add one more to the many meanings that have been given to these overworked terms. This would not matter at all if, by

universal agreement this text were taken as the sole authority on definitions for the future, or even if the reader were warned that the definitions do not correspond with general practice, but the newcomer to ecology who is under the illusion that these are generally accepted definitions will experience much confusion when he comes to read more widely.

The same rather sweeping use of new definitions is presumably responsible for the unannounced introduction of new phrases in place of well-established ones; thus the perfectly satisfactory 'intrinsic rate of natural increase' which, after 30 years' use was renamed 'innate capacity for increase' by Birch is now to be known after a further 5 years as 'unlimited rate of natural increase'. If every author is to invent his own form of words without explaining that they mean precisely the same as the cast-off expression, the student will be confused indeed. Again it is only by a very special extension of meaning of the word 'biomass' that we can balance the equation: 'assimilation = biomass − respiration' and it is evident from the context (p. 48) that by 'biomass' we are really intended to understand 'the energy content of a particular biomass'.

It is necessary to raise these points, not in order to decry an admirable book, but because they illustrate two different attitudes to this fundamental question as to whether students will be more effectively led to comprehend a subject and taught to think about it profoundly by having ready-made definitions put before them, or whether they should be forced to argue out for themselves the relative virtues of the different attitudes which these discrepancies represent in real life. It is quite possible that each method is appropriate at a different stage in the development of a science or for students at different stages of their training.

As regards the structure and presentation of the book, the author's original approach is reflected in the unusual but obviously sensible order in which the topics are discussed. The first part concerns principles, and works down from 'biogeochemical' cycles to the population and then back again to a synthesis of the community. A second section on habitats, freshwater, marine and terrestrial is stimulating despite—or perhaps on account of—a North American bias and the need to skim the cream from topics which are usually the province of whole volumes. The third part, on applied ecology, covers conservation, public health, radiation ecology and human population control with great competence and mastery of principles. There is a useful bibliography and an index which was not once found to fail.

Odum's textbook is already widely accepted as one which goes straight to the heart of the subject and avoids many of the impediments of a ridiculous jargon and of the over-emphasis on methods and taxonomy which characterize much teaching of the subject. This second edition is notable especially for the satisfactory way in which new knowledge —much of it obtained by Odum and his associates—in the field of productivity ecology has given us a wider and sometimes simpler view of the subject as a whole. It is not a book to fit in with a course on the kind of general biology which is too often called ecology, nor should it be regarded as a sole source for the advanced student, but it is a brilliant synthesis, full of information and, above all, ideas for those who wish to clarify the structure of a rapidly developing subject in their own minds.

A. MACFADYEN

Hilary B. Moore (1958). *Marine Ecology*. Pp. xi + 493; 244 text-figures. New York: Wiley (London: Chapman & Hall). Price 76*s*.

Prof. H. B. Moore's book *Marine Ecology* is concerned with all parts of the sea, from the upper levels of the shore to the deepest abyss. It deals with the ecology of the sea at a level which will be of interest to the research worker and to the advanced undergraduate

student, and to both it will prove extremely useful. It is well written, very liberally illustrated with clear tables and diagrams, and excellently produced.

The book is arranged in an ecologically methodical way. Dr Moore first describes and discusses the various physical, chemical and biological factors by which an ecologist hopes to characterize the environment –temperature, illumination, wave action, oxygen tension, inorganic salt concentrations, food, predation and many others. From examples taken from many diverse parts of the world, Dr Moore illustrates the action, complexity and interaction of these factors. Next are described the various types of environment – abyssal, the pelagic environment at various depths and also in coastal waters, and the sea bottom of the continental shelf; there are special sections on coral reefs, on various types of intertidal shore, and on estuaries. Finally, marine ecology is viewed *via* the organisms themselves, in their various habitats already described. This arrangement has the great advantage of presenting and combining the various approaches of the ecologist —assessment of the environment, general faunistic and floristic survey, and autecological studies of particular species. It involves some repetition, but this is skilfully handled and well justified. Of these various parts, perhaps the least complete is that which deals with the organisms themselves, but this is inevitable owing to the wealth and diversity of species.

This book is not a marine encyclopaedia but an instructive survey with examples. It should therefore not be criticized for omissions, unless these are of important studies of a type not otherwise satisfactorily represented, or of work which would usefully qualify and amplify topics chosen by the author for discussion. The book is a well-balanced and very useful survey, and the criticisms which follow will not alter this fact.

The outstanding defect of this book is that it is out of date. The number of references falls off severely from 1950 onwards, and very little has been included after 1952. The insertion of a few book titles and references to *Deep Sea Research* in 1956 does not redeem the situation. Many of the criticisms offered below are to be explained on the assumption that Dr Moore gave up the unequal struggle with the literature in 1952.

The author emphasizes the importance of physiological ecology and deplores the lack of knowledge in this branch of the subject. The description of the situation in the 'field' must come first. Marine ecologists are now beginning to apply experimental methods both in the 'field' and in the laboratory; a still more remote stage will be the physiological investigation of the empirical information so obtained. Dr Moore has not quite taken full advantage of the physiological possibilities of his subject. His necessarily brief excursions into osmoregulation, diving physiology and high pressure, are superficial; and he has overlooked some important fairly recent contributions to physiological ecology.

Dr Moore successfully expounds an ecologist's belief that the characteristics of the environment must ultimately be analysed in terms of a number of 'factors', some more and some less important, acting on all stages of the life history and on all aspects of the biology of the organisms concerned, and interacting and modifying each other's effects. For instance, in describing the effects of temperature, which he rightly regards as of outstanding importance, he discusses Hutchins's interpretation of the effects of temperature on geographical distribution, gives examples of lethal extremes, and goes on to describe less drastic effects on reproductive physiology, growth, feeding and so forth. Other factors are treated similarly although some of these rather briefly. Illumination is reviewed interestingly in relation to algae, and there is a valuable section on the action of waves. Biological environmental factors might seem to merit more attention.

The conditions in the various marine environments are described in terms of environmental factors in Chapters 5 and 6. Physical and chemical conditions in the abyss are briefly described, and there is an attempt to estimate the food supply there. There is valuable discussion on illumination in the upper oceanic waters, with interesting ideas

about the possible importance of moonlight in guiding planktonic migration, and attention is drawn to the possible importance of the rate of change of a factor such as illumination in stimulating behavioural responses. Physical and chemical conditions in oceanic and coastal waters, on various types of shore, and in estuaries, are excellently described. Lochs and fjords might have received a brief mention as such, with reference to Scandinavian authors such as Strøm.

The second half of the book is taken up with the ecology of marine organisms, habitat by habitat. It is a section full of interest but impossible to summarize. Rightly the plankton once more receives very full attention. Among other things, Dr Moore discusses the combined effect of illumination and temperature in limiting downward migration. He mentions the exclusion hypothesis without reference to R. Bainbridge's (1953) laboratory experiments, and also overlooks J. E. Harris's contributions to the significance and mechanism of migrations. There is a chapter on inshore fisheries; although, in spite of the author's plea for 'integral ecology', D. H. Cushing (1955) has been ignored. Curiously also, there is no mention of the work of J. E. G. Raymont and his collaborators on the enrichment of sea lochs with fertilizers.

In the section on the shore Dr Moore gives a useful account of the various tidal levels which are likely to be critical. Zonation is the outcome of tidal and other modifying influences acting upon organisms through most or all of their life histories. Dr Moore has been a pioneer in demonstrating how the whole biology of organisms (including such features as growth-rate and reproductive pattern), may be affected by tidal level. He does not discuss in this book the importance of behaviour mechanisms in keeping a motile intertidal organism at its appropriate level, as for instance by reference to gastropods or sand hoppers. Interesting literature on the physiology and behaviour of barnacles since 1951 could also have been discussed. The fact that not one species of Porifera is mentioned throughout the book is a reflection on marine ecologists in general rather than on Dr Moore.

This is a valuable book by an author experienced in work on the shore and on the open ocean; the next edition should be invaluable.

J. A. KITCHING

EXPLOITATION OF THE SEA

L. A. Walford (1958). *Living resources of the sea: opportunities for research and expansion.* Pp. xv+321; 23 maps. New York: Ronald. Price $6.00.

This book is the author's attempt to answer a question put to him by the Conservation Foundation: 'What scientific researches, apart from those which are now in progress, would contribute significantly towards learning how to enlarge the yield of food from the sea in answer to human needs?' Dr Walford's answer makes remarkably stimulating reading. When he made this study he was Chief of the Branch of Fishery Biology in the U.S. Fish and Wildlife Service, and this position, considered together with his activities as scientific adviser to delegations of his Government to several international fisheries commissions, gave him opportunities such as have come to few other fisheries scientists to feel the pulse of their subject. He has been able to take the very broad view and yet at the same time explore some dark corners to advantage.

This book is therefore informative, authoritative and, as acquaintance with Dr Walford would lead one to expect, highly individual. Some manifestations of this last characteristic will surprise ecologists. Thus one of the most important chapters of the book is that entitled 'Environment', which is defined early on as a 'habitat together with its resident communities of plants and animals', that is to say, it is regarded as synonymous with the aquatic 'ecosystem'. But there is no need for concern; the author writes,

most of the time, about environment in the more usual sense, as something outside, around and reacting with something else—usually the commercially exploited fishes. When he remembers his original definition the context usually, but not always, makes his meaning clear. This example, and there are others, will indicate, I believe, that if the reader is looking for suggestions that will lead ecology more nearly to approach an exact science, he must look elsewhere. This book is not a monograph on either fisheries biology or ecology; nor is it a textbook. It is more a group of essays, some exciting, others, in my opinion, indifferent or distinctly dull, which nevertheless will provide for some time to come a fund of ideas for investment of money and of scientific talent to gain understanding of the physico-chemical and, particularly, biological processes in the oceans with a view to using their products to human benefit.

The book consists of two parts. The first part, headed 'The Marine Wilderness', contains most of the material of interest to ecologists. The seas are regarded as a largely unexplored, relatively unexploited wilderness, at the edges of which man is making encroachments as he might have made clearings or cultivated patches in primeval forest. Individual chapters in this part deal with a wide range of topics, without, seemingly, a logical order—marine taxonomy, environmental influences, ecological principles, fish behaviour, plankton studies and harvesting, brackish-water fish culture, fish diseases, poisonous fishes, improvement of fishing craft and gear. On all these subjects, Dr Walford has something interesting to say, though much less on, say, fishing boats than on ecological principles or plankton harvesting, and no connection is made between the discussion, in the 'Behaviour' chapter, of instruments and methods of observing fish in their habitat, and the problem of designing new or improved fishing gear, based on the results of behaviour studies. Part I contains also a chapter on 'Conservation' which does describe in a general way the biological principles on which regulation and management of marine fisheries are based. The international commissions are listed and there is some discussion of the difficulties faced by scientists working for or with those bodies—the tremendous pressures of work for too few people, the need to solve immediate practical questions and yet keep one's sights on the long-term ends—and of the social and economic problems their existence is creating. There is, however, to my mind, too little recognition of the actual and potential unifying effect for fisheries science of the present concentration on population studies for management purposes; nor of the fact that fulfilment of the other dreams—increasing productivity, transplanting, breeding, herding, culturing marine stocks—depends on successful establishment of a regime of peaceful and rational exploitation of existing stocks by international agreement. The resources of the sea may remain common property, but the nations and their fishermen will have to learn how to behave, individually and collectively, through creation of and obedience to international law, as if they were responsible owners of these resources. Until then we may expect the pattern of past trends in the north-east Atlantic to be repeated elsewhere; improvements in vessels and gear, in economic efficiency, potential improvements in the yield of the resources by breeding, transplanting and so on, will be offset by increased fishing so that in the end the same or less catches are taken but with greater trouble and expense. No one would put much effort into breeding high yield beef cattle in an agricultural society in which calves are slaughtered soon after birth, and it is difficult to envisage the funds arriving in the required quantities to execute projects of the kind many fisheries biologists have considered, and which Dr Walford has so well collected and described, unless there is soon some guarantee that the benefits from them will not be immediately whittled away by competitive fishing. It is for this reason that I believe Dr Walford might usefully have explored this question in much more detail.

The second part of the book, 'The Resources of the Sea', has chapters describing briefly the history of industries for catching, collecting and using various invertebrates, fishes, reptiles, whales, seals and seaweeds. These usefully bring together statistics of various

kinds, discuss the possible factors limiting the expansion of these industries, and the kinds of research which might modify those factors.

I have left until the end mention of what are in some ways the most interesting and suggestive sections of this book—the twenty-three maps of the world, all drawn to the same scale on an elliptical equal area projection, which present in easily comparable form information ranging over basic productivity measurements, currents, topography, world population, fish production, areas of protein starvation, accessibility of areas to surface transport, sizes of merchant and fishing fleets, numbers of oceanographic stations occupied since research began, location of marine laboratories, marine climate and weather in relation to practicability of fishing in various seasons, location of coral, distribution of biological groups and species. I thought it would have been better if more such charts were available, on a larger scale, and printed on transparent paper to facilitate comparison; I find that the author has anticipated this, and we may expect that the *Journal of Atlantic Biogeography* which, with Dr Walford's initiative, is being launched by the American Geographic Society, will produce just that.

To summarize, this is a most valuable book, written by a biologist and scientific administrator with a keen sympathy for and deep understanding of the ecological viewpoint. It will amply repay reading by ecologists, whether or not they are personally connected with marine or freshwater research. But they should read it soon; some of the proposals in it are already becoming fact, due in no small part to the activities of its author.

There is, unfortunately, no conventional bibliography, but references and notes are assembled, chapter by chapter, at the end of the book. There is an index, which includes subjects, common and scientific names, and names of scientists and others mentioned; it is adequate but far from exhaustive. The last chapter, entitled 'Looking Forward', concludes that a great deal of money needs to be spent on the study of the oceans, and, even more important, far more scientists specialized in all manner of disciplines, are needed to make this study. With that, few marine biologists, fisheries scientists, or ecologists will disagree.

S. J. HOLT

BRACKISH WATERS

A. Remane & C. Schlieper (1958). *Die Biologie des Brackwassers* (*Die Binnengewässer*, Bd. XXII). Pp. ix+348; 139 text-figures. Stuttgart: Schweizerbart. Price DM 55.00.

One of the attractions which the study of brackish waters has for the ecologist and physiologist is the apparent simplicity of the variable factors involved. We have available for investigation a graded sequence of aquatic environments differing from each other in one main factor, salinity, which can be easily measured and reproduced in the laboratory for experimental purposes. It would seem that here is an ideal field for combined ecological and physiological research which should lead to a clear understanding of the mechanisms of adaptation and of the causes of the distribution of species within a limited range of conditions. It need hardly be said that in practice the matter is not as simple as that, but it is certainly true that the composition of the fauna and flora of brackish waters is determined primarily by salinity, and that salinity is the only basis upon which a useful biological classification of such waters can be made.

Professor Remane in his discussion on 'Ökologie des Brackwassers', which occupies two-thirds of this book, brings together a great deal of information which had been widely scattered through the literature. The contexts in which the subject matter is discussed are the definition, classification and origin of brackish waters, ecological peculiarities of

the organisms and their origin, conditions of life in these waters, and some particular examples of brackish water environments. In the last section is a fascinating discussion of the history, hydrography and ecology of the Baltic and Ponto-caspian waters. The small amount of work done as yet in the tropics will soon, we hope, be much augmented.

A number of unsolved general problems will occur to the reader. One of these, which is mentioned by Professor Remane, is the inadaptability, in spite of an ultimate marine origin, of most freshwater animals to any but a minimal salinity in which they have evolved with phenomenal success. Brackish waters have in fact been colonized mainly from the sea, but the problem is further complicated by the fact that a certain number of freshwater animals have become adapted to inland saline waters where salinity is liable to be even higher than in brackish water or the sea. It is also surely remarkable that the radical changes in the physiological make-up of an organism needed for adaptation to a widely different range of salinity has occurred on innumerable occasions during the course of evolution. Within the same small taxonomic group, even the same genus (e.g. *Diaptomus*, *Cyclops* and *Nitocra*) there are species which are confined to fresh water and others which can tolerate extremely high salinities.

We are still a long way from understanding these and similar problems, as a study of the section by Professor Schlieper on 'Physiologie des Brackwassers' will show. In this is reviewed what is known of the mechanisms for osmotic and ionic regulation in brackish water animals with subsidiary discussions on the effect of temperature and the relation of respiration to the regulatory mechanisms. Most of the significant work in this field is discussed, but the value of the book would have been enhanced by some discussion, however tentative, of the relevance of the physiological to the ecological findings. What light does physiology throw on the origin of the fresh, brackish and inland saline water faunas and what are the gaps in our knowledge which must be filled in order to understand these problems better?

The reader will turn in hopeful anticipation from Professor Remane's section in which these challenging problems are raised but will be disappointed to find that the subject matter of Professor Schlieper's comprehensive review has not been presented with the object of unifying the book as a whole. The opportunity has been missed for presenting a physiological ecology of brackish waters which would have been more satisfying to the general reader and stimulating to the specialist wishing to understand the wider significance of his work.

L. C. BEADLE

SEWAGE POLLUTION AND FISH

I. R. H. Allan, D. W. M. Herbert & J. S. Alabaster (1958). *A field and laboratory investigation of fish in a sewage effluent.* Fish Invest. (1) **6,** No. 2, pp. lx + 76. London: H.M.S.O. Price 21*s*.

This is an important study which will be of interest to all ecologists who are concerned with the biology of rivers, and will also do much to clarify the position for fishermen and the many other people who wish to enjoy the amenities offered by rivers in populous areas.

The authors studied, by means of trapping and by experiments on caged fish, the effect of the effluent from a modern sewage works on several species of fish, and they also carried out an extensive programme of laboratory experiments in order to establish which chemical and physical properties of the effluent were important to the fishes.

The area chosen for the field work was the effluent channel leading from the Colne Valley sewage works into the River Colne, which, like so many English lowland rivers,

is a complex of channels. A result of this complexity was that below the outfall there was a channel nearly a mile long containing usually only pure sewage effluent. This channel was, at its lower end, in free communication with a large area of clean water from which fishes could move into it. In this respect conditions were a little unusual in that there was a reservoir of fishes which was constantly available to colonize the most seriously polluted reach, but this situation was very well suited to the objects of the investigation.

Four species occurred commonly, namely roach, perch, gudgeon and tench; they were at times abundant in the channel, which contained a typical 'pollution' flora and invertebrate fauna on which they were feeding. Regular trapping, and some marking experiments, showed that the fish moved into and out of the area in a fairly regular manner. Roach, perch and tench moved in during the summer and out during the winter, as they did also in the nearby reaches of the river. Gudgeon were present at all seasons, and, during the two years of the investigation, increased markedly in numbers. The seasonal movements were shown to be part of the normal behaviour of the fish and nothing to do with the effluent.

In the channel, fishes often died in the traps and the records of these occasions, together with experiments in which rainbow trout were confined in cages, form the data of the effects of the effluent.

Physical and chemical investigations showed that the concentration of oxygen was higher at the top of the channel than at the lower end, and that the difference was greater at times of lower flow or higher temperature. The concentration of un-ionized ammonia varied widely and rapidly but was usually less than 10 parts per million (as N). Free carbon dioxide also fluctuated but was usually between 25 and 30 p.p.m. Concentrations of metals and detergents were generally low.

The laboratory studies, like the cage experiments, were made with rainbow trout, and some of them have already been published elsewhere. In this paper, however, they are brought together and discussed with special reference to sewage pollution. They showed that there was a great deal of complex interaction between the various properties of sewage effluents. Thus, quite small amounts of carbon dioxide increase the susceptibility of fishes to lack of oxygen, which itself increases the toxicity of un-ionized ammonia. The toxicity of ammonia is, however, much reduced by the presence of carbon dioxide, which, by lowering the pH causes the formation of the much less toxic ammonium ion. It therefore gives protection against ammonia poisoning up to values of about 30 p.p.m. CO_2, at which concentration the toxicity of the carbon dioxide itself begins to be important. The experiments also show that while detergents and metals were not present in the effluents in concentrations likely to kill fishes, they did increase their susceptibility to lack of oxygen.

Working on this firm basis of experimental data the authors attempt to explain the results of their field observations on the death of fishes in cages and traps. They found that in the field the toxicity of ammonia and the susceptibility to lack of oxygen were greater than in the laboratory tests. For the first finding they offer no explanation, but the second is satisfactorily accounted for by the interaction of carbon dioxide and oxygen. The former gas therefore raises the lower tolerable concentration of oxygen, but it also gives protection against ammonia. The general conclusion is that oxygen content is the most important factor controlling the suitability of sewage-polluted water for fishes, but that carbon dioxide and ammonia are important subsidiary factors, detergents and metals being probably less important. The authors, and the Ministry of Agriculture and the Water Pollution Research Laboratory who sponsored the investigation, are to be congratulated on having produced such a clear answer to one of the central problems of pollution.

H. B. N. HYNES

NATURAL HISTORY OF THE SALMON

J. W. Jones (1959). *The Salmon.* Pp. xvi+192; 27 plates; 24 text-figures. London: Collins (New Naturalist Special Volume). Price 18*s*.

Nowadays the life history of the salmon has become part of our cultural heritage. Almost everyone knows the broad outline of the story, but our knowledge is surprisingly incomplete; there is still much to be discovered about the life of the fish in the river, where it is pretty accessible, and of its life in the sea we are almost wholly ignorant. The salmon is in fact a very difficult subject for research. It suffers from the disadvantages that it is a very expensive and palatable fish which is, at the same time, the object of an extremely popular sport. It is therefore surrounded by a cloud of vested interests which are so complicated that the organization of any programme of research and experiment is a major diplomatic feat. A minor difficulty is that the fish are retailed ungutted and accordingly even what is known as 'offal' is hard to come by for study. For this reason salmon studies have to a large extent been distorted. They have been restricted to direct observation of the fish under very difficult circumstances, to marking experiments and to studies in age and growth deduced from scales which can be obtained quite readily because their removal impairs neither the live nor the dead fish. Dr Jones has made for himself better opportunities than these and has used them most successfully. He has made detailed studies of the young stages of salmon and has improved on the observational technique by studying the fish in a glass-sided tank which was in fact part of a natural river.

In very many ways his book is a great advance on anything about the salmon that has appeared before. The prize chapters are, of course, those relating to the spawning of adult fish and to the spawning of the male parr. It looks as if the salmon could easily become a species consisting of large anadromous females and small freshwater males and that this is only being prevented by a rigid behaviour pattern is a matter of great importance and requires following up. For instance, can large female trout spawn with small males or is this the mechanism which keeps sea trout racially distinct from brown trout, if indeed they are?

As the chapter headings indicate ('Young Salmon in the River', 'The Salmon in the Sea', 'The Homing Instinct and the Return to the River', 'The Return to the Sea') Dr Jones concentrates mainly on the life history of the fish and he does it well. By his own work and particularly by his critical use of the scale-reading technique (Chapter 3) he has made useful discoveries about the life of the young salmon in rivers and he has gathered together in a convenient form all the reliable information there is about the other stages.

Yet, to the ecologist, the book is bound to be a disappointment. A knowledge of the life history of any organism is of course fundamental to a study of its ecology, and in that respect we shall find the book invaluable. But it is far too short and Dr Jones has barely indicated the outstanding ecological problems associated with the salmon. What, for example, are the population dynamics of the species and what are the controlling factors? (Except locally and occasionally they are certainly not principally human, as the first and last chapters suggest.) What is the relation between size and migratory habit? (It is mentioned in the case of smolts, but why should some rivers always be populated almost solely by small grilse and others by larger and older fish?) How does a species with so strong a tendency to return to its natal river manage to maintain its apparent genetic uniformity over so wide an area?

It is true that these questions are unanswerable at present, but there is some information about them all and a discussion of them by Dr Jones would be illuminating and valuable. Could not the next edition be twice the size and broader in scope?

The book is well produced, as befits the New Naturalist series; the illustrations are good, misprints and minor errors commendably few.

F. T. K. PENTELOW

ACAROLOGY

T. E. Hughes (1959). *Mites: or the Acari.* Pp. viii+225; 52 line drawings. London: Athlone Press. Price 42*s*.

Although not primarily about ecology, this book is of great potential value to the steadily increasing number of ecologists who work with soil invertebrates. Further, it can hardly fail to appeal to the general biologist's feeling—surely not yet dead for the beauty of animal form as revealed by first-class illustration. For anyone who identifies mites the book brings together background information on the functions and detailed structure of parts and organs, which is only accumulated piecemeal and imperfectly in the normal course of events. Although the author modestly acknowledges his debt to H. Graf Vitzthum, his book apart from obvious advantages of price and language contains much that is new, reviews a wider range of world acarology, and contains fewer errors than Vitzthum's classic work. For the newcomer to mite taxonomy this is a readable and enthusiastic introduction to the subject.

The acari have associations with the majority of other animal groups and also include important plant pests; perhaps the most widely useful parts of the book will be the important chapters on this subject. These are arranged by habitat and then by taxonomic position of host organisms, and there can be few biologists, whether acarologists or not, whose conception of the biological significance of the Acari will not be broadened by reading this part of the book.

The production of the book and the value, by modern standards, are excellent; the only criticism I would make, in view of there being more than fifty (unlisted) plates, is the frustrating absence of page references in conjunction with the quotation of plate numbers in the text.

A. MACFADYEN

BOOKS RECEIVED

Handbook of computations for biological statistics of fish populations by W. E. Ricker. Bull. Fish. Res. Bd. Can. No. 119. Ottawa. 1958. Price $5.80.

Planning of Experiments by D. R. Cox. New York: Wiley (London: Chapman & Hall). 1958. Price 60*s*.

Environmental Conservation by Raymond P. Dasmann. New York: Wiley (London: Chapman & Hall). 1959. Price 52*s*.

Practical Animal Ecology by W. H. Dowdeswell. London: Methuen. 1959. Price 32*s*. 6*d*.

The earthworm fauna of New Zealand by K. E. Lee. Wellington: Govt. Printer (N.Z.D.S.I.R. Bull. No. 130). 1959. Price £3.

Oceanography and Marine Biology: a book of techniques by H. Barnes. London: Allen & Unwin. 1959. Price 35*s*.

Apparatus and Methods of Oceanography. Part One: Chemical by H. Barnes. London: Allen & Unwin. 1959. Price 40*s*.

The principles of experimental technique by W. M. S. Russell & R. L. Burch. London: Methuen. 1959. Price 30*s*.

The Cellular Slime Molds by J. T. Bonner. Princeton, N.J.: Princeton Univ. Press. 1959. Price 32*s*.

Key to the names of British butterflies and moths by R. D. Macleod. London: Pitman. 1959. Price 15*s*.

Fundamentals of Ornithology by J. van Tyne & A. J. Berger. New York: Wiley (London: Chapman & Hall). 1959. Price 94*s*.

Adventure of the Air by James Fisher. London: Rathbone. 1958. Price 17*s*. 6*d*.

Proceedings of the New Zealand Ecological Society, No. 6. Wellington: P.O. Box 202. 1959. Price 7*s*. 6*d*.

ABSTRACTS

The abstracts are edited by Professor L. A. Harvey with the assistance in selecting and abstracting of J. D. Brayshaw, G. I. Crawford, T. A. W. Davis, A. E. Ellis, F.A.O., Fisheries Division, P. D. Gabbutt, D. Leatherdale, A. Macfadyen, C. Matheson, E. J. Moynahan, Miss E. Nelmes, W. R. Pickering, J. L. Cloudsley-Thompson, Mrs M. Vincent and W. B. Yapp. References are checked by B. M. Hobby. Mr R. S. R. Fitter, with the help of the societies themselves, aims to cover all the proceedings, transactions and journals of local natural history societies and field clubs. Secretaries of such organizations are urged once again to aid this work by making sure that copies of their publications are sent, regularly, to **R. S. R. Fitter, Esq., Drifts, Chinnor Hill, Oxford.** Readers and authors can materially assist by pointing out errors and omissions, and by sending reprints or offers of help in making abstracts to **Professor L. A. Harvey, The University, Exeter.**

Separate copies of the abstracts suitable for mounting on cards can be obtained from **Blackwell Scientific Publications Ltd., 24-25 Broad Street, Oxford,** or through any bookseller; price 5*s*. 6*d*. per annum, post free (issued in May and November). Back numbers of the 'Notices of publications ... ' from Vol. 3 (1934) to Vol. 20 (1951) may also be had at 2*s*. for each annual set of two parts.

CONTENTS

Note. In order to avoid unnecessary overlap with journals which the ecologist would be likely to consult in any case, papers in the *Journal of Animal Ecology* are not noticed, nor are:

(*a*) papers in *British Birds* which would fall in '4. Food and food habits';

(*b*) papers in the above journal and in *The Entomologist's Record* and *The Entomologist's Monthly Magazine* which would be classified in '5. Migration, introductions and local distribution'.

PAGE

1. Ecological surveys and the relations of animals to habitat conditions 396
   (*a*) Marine and brackish 396
   (*b*) Fresh water 396
   (*c*) Land 397

2. Methods, apparatus, population statistics and taxonomic studies of use to ecologists 401

3. Parasites 405

4. Food and food habits 406

5. Migration, introductions and local distribution . . . 407

6. Studies on behaviour 408

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Gibson, F. A. (1956). Escollops (*Pecten maximus* L.) in Irish waters. *Sci. Proc. Roy. Dub. Soc.* **27,** 253-270.

Escollops commercially caught from the two main fishing grounds in Ireland were examined. A successful method of tagging was developed. Although replacement seems adequate, natural and fishery mortalities appear high.

Hancock, D. A. (1958). Notes on starfish on an Essex oyster bed. *J. Mar. Biol. Ass. U.K.* **37,** 565-589.

Distribution, settling, feeding habits and growth of *Asterias rubens* and *Solaster papposus* on oyster beds.

Mason, J. (1958). The breeding of the scallop, *Pecten maximus* (L.) in Manx waters. *J. Mar. Biol. Ass. U.K.* **37,** 653-671.

Describes gonads, breeding cycle, spawning and fertilization and analyses numbers of larvae and spat.

Millar, R. H. (1958). The breeding season of some littoral ascidians in Scottish waters. *J. Mar. Biol. Ass. U.K.* **37,** 649-652.

Distinguishes north and south boreo-arctic and boreal species and discusses the times and durations of their breeding seasons.

Walne, P. R. (1958). Growth of oysters (*Ostrea edulis* L.). *J. Mar. Biol. Ass. U.K.* **37,** 591-602.

Relations between growth in length and weight of oysters at Tal-y-foel and mean monthly temperatures, tidal exposure and salinity.

(*b*) Fresh water

Butler, P. M. & Popham, E. J. (1958). The effects of the floods of 1953 on the aquatic insect fauna of Spurn (Yorkshire). *Proc. R. Ent. Soc. Lond.* (*A*), **33,** 149-158.

Lists the species (Diptera, Trichoptera and Gerroidea excluded) collected from a range of low-to-high salinity habitats. Observed changes in the fauna are mainly due to salinity changes. Flooding results in the elimination of the stenohaline species and the euryhaline species, with good powers of migration, become temporarily dominant. With the return of the stenohaline species the euryhaline species remain dominant only in the more brackish habitats.

Corbet, P. S. (1958). Temperature in relation to seasonal development of British dragonflies (Odonata). *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 755-757.

The process of synchronization involves two ecological demands, (*a*) the need for the population to pass the winter in a resistant stage and (*b*) the need for the reproductive stage to be restricted to the warm season. Concludes that the fundamental difference between spring and summer species is that the former achieve synchronization when temperatures are falling and the latter when they are rising.

Mann, K. H. (1958). Annual fluctuations in sulphate and bicarbonate hardness in ponds. *Limnol. Oceanogr.* **3,** 418-422.

Seasonal fluctuations in four ponds suggest reduction of sulphate to ferrous sulphide which becomes locked in mud; carbonate changes seem to be due to removal of CO_2 by photosynthesis and the action of sulphuric acid when sulphides are oxidized in winter.

Reynoldson, T. B. (1958). Observations on the comparative ecology of lake-dwelling triclads in southern Sweden, Finland and northern Britain. *Hydrobiologica,* **12,** 129-141.

Several British lake triclads are absent from Sweden and Finland, notably *Polycelis nigra* and *P. felina*. *Dendrocoelum lacteum* in Sweden occupies the place of *P. nigra* in British waters. As here, so in Sweden a strong correlation exists between triclad faunas and the chemical characteristics of lake waters.

Scott, D. & Rushforth, J. M. (1959). Cover on river bottoms. *Nature, Lond.* **183,** 836-837.

Discusses use and limitations of stones as parameters in river ecological studies.

(*c*) Land

Anon. (1958). Island of Skomer, description and history. *Nature in Wales,* **4,** 663-694.

A general account of the topography, history and natural history of Skomer Island on its establishment as a National Nature Reserve, to be occupied and managed by the West Wales Field Society.

Barnes, H. F. (1958). Wheat blossom midges on Broadbalk, Rothamsted Experimental Station, 1927-56. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **3,** 367-374.

Shows that an assessment of the larval population should be based on floret, not ear, infestations and describes the periodicity of two species, *Contarinia tritici* and *Sitodiplosis mosellana* and their parasites.

Betts, M. M. (1958). Notes on the life-history of *Ernarmonia conicolana* (Heyl.) (Lep., Eucosmidae). *Ent. Mon. Mag.,* **94,** 134-137.

The larvae of *E. conicolana* live in pine cones and are an important winter food for blue tits. Eggs were laid on one year pine cones where the larval instars develop, pupation takes place in the tip of the cone. No distortion of the cones was found.

Bevan, W. J. & Uncles, J. J. (1958). Studies on soil population of *Contarinia pisi* Winn. in 1957 in Yorkshire and Lancashire. *Ann. Appl. Biol.* **46,** 529-535.

Emergence data related to soil populations of pea-midge pupae in fields that had carried peas in 1956 and in fields under peas in 1957. There were indications that increases of temperature might accelerate pupation, with resultant earlier emergence.

Birch, L. C. (1957). The role of weather in determining the distribution and abundance of animals. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 203-218.

Discusses fluctuations of grasshopper, bird and mammal populations in relation to weather, and postulates a stochastic model emphasizing the instability of natural populations.

Blake, G. M. (1959). Control of diapause by an 'internal clock' in *Anthrenus verbasci* (L.) (Col., Dermestidae). *Nature, Lond.* **183,** 126-127.

The life-history of this beetle in southern England is described. The cycle of rapid growth in summer and rest in winter persists when development occurs under constant physical conditions. Humidity, carbon-dioxide concentration, temperature and illumination were controlled during the experiments.

Boase, H. (1959). Shelduck counts in winter in East Scotland. *Brit. Birds,* **52,** 90-96.

Counts at Edenmouth, Fife, Montrose Basin, Angus and Kingoodie, Perthshire, show a succession of movements early in the year. Very few first-year birds are recorded in winter. Results of counts in the three localities are shown on diagrams.

Bone, Q. & Hardy, M. G. (1958). Some observations upon a polymorphic population of *Argynnis paphia* (L.) (Lep., Nymphalidae) in the New Forest. *Ent. Mon. Mag.* **94,** 114-119.

Results of the first season's observations are discussed; the work will continue for several more seasons. From these first results the percentage of the recessive gene '*valesina*' in the females is 5·69%.

Cawthra, E. M. (1958). The occurrence of *Cleonus piger* Scop. (Col., Curculionidae) at Aberlady Bay, East Lothian, with some notes upon its larval instars. *Ent. Mon. Mag.* **94,** 204-206.

This weevil is found on sand dunes at Aberlady Bay. The larvae burrow into the stems of the thistle *Cirsium arvense,* and develop there. Eggs are usually laid in the sand very close to a thistle plant.

Chant, D. A. (1958). On the ecology of typhlodromid mites in south-eastern England. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **4,** 649-658.

Describes the relationship between *Typhlodromus tiliae* and the European red mite *Metatetranychus ulmi* and shows that the predator is relatively ineffective as the two species inhabit different locations.

Chapman, R. F. (1958). Notes on the biology of *Hylesinus fraxini* (Pz.) (Col., Scolytidae). *Ent. Mon. Mag.* **94,** 245-247.

The pattern of the galleries of the ash bark beetle are described and related to its development.

Chitty, D. (1957). Self-regulation of numbers through changes in viability. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 277-280.

Discusses problems associated with the severe mortality commonly affecting populations of *Microtus* spp.

Clark, K. K. (1959). Honeybees in the orchard. *Agriculture,* **65,** 572-575.

Efficiency of honeybees in pollination can be increased by removal of rival plants and interplanting of pollinators.

Collyer, E. & Kirby, A. H. M. (1959). Further studies on the influence of fungicide sprays on the balance of phytophagous and predacious mites on apple in south-east England. *J. Hort. Sci.* **34,** 39-50.

The effects of fungicide programmes, particularly lime-sulphur and captan, on populations of fruit-tree red spider (*Metatetranychus ulmi*) on Cox's orange pippin were studied for five consecutive seasons. Levels and fluctuations of predacious mites (notably *Typhlodromus tiliae*) and insects (*Anthocoris* spp., *Orius majusculus* and *Blepharidopterus angulatus*) were recorded, and the data give support to the idea that *Typhlodromus* mites are an important factor in the control of *M. ulmi*.

Davies, M. (1959). A contribution to the ecology of species of *Notiophilus* and allied genera (Col., Carabidae). *Ent. Mon. Mag.* **95,** 25-28.

A summary of published work on the ecology of *Notiophilus* and other related ground beetles, with additional data collected from further ecological work on these beetles.

Edney, E. B. (1958). A new interpretation of the relation between temperature and transpiration in Arthropods. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 329-332.

An evaluation of recent work shows that where transpiration occurs through non-waxed areas little, or no, temperature effect is observed, whereas an approximately exponential temperature dependence results from transpiration through a complete or feebly porous wax layer, the precise nature of the relationship depending upon the degree of porosity.

Edney, E. B. (1958). The micro-climate in which woodlice live. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 709-712.

Gives details of microclimatic measurements and observations at two habitats in England and Algeria containing a number of named woodlice species.

Fletcher, J. R. (1959). Starling roosts in young plantations. *Quart. J. For.* **53,** 58-60.

Roosting of starlings in a Sitka spruce plantation in a catchment area resulted in grossly polluted run-off water necessitating drastic measures to induce the birds to leave. Notes preferences for 20-25 ft trees and for unbrashed areas.

Gillham, E. H. (1958). Further notes on the tufted duck in St. James's Park, London. *Brit. Birds,* **51,** 413-426.

Observations on the proportion of the sexes, the moult of females, the departure of males for moulting grounds, parental care and fledging period. The average mortality of ducklings was 50%. More than half died in the first 7 days, especially in cold wet weather.

Goodacre, M. J. & Lack, D. (1959). Early breeding in 1957. *Brit. Birds,* **52,** 74-83.

Seven resident passerine species and the tawny owl laid eggs 6-12 days earlier than usual, and other resident species almost certainly did so. Some summer visitors nested a little early, others did not. The winter and early spring were very mild in 1957, and temperature may act directly on birds.

Gould, H. J. & Legowski, T. J. (1959). Timing sprays for control of pea moth. *Agriculture,* **65,** 611-614.

Jordan, A. M. (1958). The life history and behaviour of *Coleophora alticolella* Zell. (Lep.). *Trans. Soc. Brit. Ent.* **13** (1), 1-16.
This species is found in moorland in the northern Pennines from early June to mid-July during which period oviposition occurs. The larvae feed on the seed capsules of *Juncus* spp. and *Luzula campestris*. Four larval instars occur, cased larvae overwinter and pupate in the spring.

Kettlewell, H. B. D. (1958). Industrial melanism in the Lepidoptera and its contribution to our knowledge of evolution. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 831-841.
Shows that birds are responsible for a differential selection, moths being taken in order of their conspicuousness, by eliminating white moths in polluted areas and black forms in unpolluted areas. This single factor accounts for the spread of melanic forms throughout central and eastern England.

Kettlewell, H. B. D. (1958). The importance of the microenvironment to evolutionary trends in the Lepidoptera. *Entomologist,* **91,** 214-224.
Includes the results of experiments and observations with polymorphic species demonstrating ability in the different forms to select backgrounds suitable to their colouring.

Kontkanen, P. (1957). On the delimitation of communities in research on animal biocoenotics. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 373-378.

Mackenzie, J. M. D. (1959). Roosting of treecreepers. *Bird Study,* **6,** 8-14.
A summary of replies to a request for data. Various sites are used, but general preference is noted for crevices in the bark of *Wellingtonia*.

Miles, M. (1958). The contribution of biological studies to the control of Anthomyiid flies of economic importance. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **3,** 111-114.
A comparative study of the life histories of *Hylemyia brassicae, floralis, antiqua, cilicrura* and *brunnescens*.

Miles, H. W. (1958). Dock sawfly. An occasional pest of apples. *Agriculture,* **65,** 402-405.
Life history and control methods described.

Milne, A. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). 2. The cycle from egg to adult in the field. *Bull. Ent. Res.* **47,** 23-42.
Description of 1 year life-cycle in the Lake District, with methods of feeding and analysis of population structure.

Milne, A. (1958). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). 4. The flight season: introduction and general aspects. *Bull. Ent. Res.* **49,** 685-699.
Feeding and swarming activities described in relation to time of day, season and vegetation patterns.

Milne, A. & Laughlin, R. (1956). Biology and ecology of the garden chafer, *Phyllopertha horticola* (L.). 1. The adult and egg production. *Bull. Ent. Res.* **47,** 7-22.
In the laboratory egg production depends on fat stored by the third instar larva before hibernation, not on adult feeding. Oviposition, length of life, incubation, etc., are discussed.

Ollerenshaw, C. B. (1958). Climate and liver fluke. *Agriculture,* **65,** 231-235.
Epidemics may be forecast from the weather.

Olsson, V. (1958). Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus*. A study based on recoveries of birds ringed in Fenno-Scandia. *Acta Vertebratica*, **1** (2), 89-189.

An important survey of ringing recoveries of tawny owl, buzzard, heron and herring gull ringed in Finland and Scandinavia. Rates of abrasion of rings are too low to affect results except from herring gulls after 6-7 years. Migrations and dispersal of the birds over eastern Europe are described and compared with relation to the ecological needs of each species. Causes of death are analysed; average expectations of life calculated. Mortality rates are more than balanced by survival rates.

Perrins, C. M. (1959). Jay killed by weasel. *Brit. Birds*, **52**, 60-61.

The weasel attacked from behind, and fought for 30-45 seconds before it secured a fatal grip at the back of the jay's neck.

Picther, R. S. (1958). The biology of the black currant leaf midge *Dasyneura tetensi* (Rübs.) in relation to the planning of control measures. *Rep. East Malling Res. Stn.*, **A41**, 136-139.

Suggestions for improving future control of the midge are made as a result of this study of its life history.

Smith, K. V. G. (1959). The distribution and habits of the British Conopidae (Dipt.) *Trans. Soc. Brit. Ent.* **13** (7), 113-136.

Thompson, J. L. Cloudsley- (1958). The effect of wind upon the nocturnal emergence of woodlice and other terrestrial arthropods—1. *Ent. Mon. Mag.* **94**, 106-108.

Wind speeds and relative humidity are shown to affect the activity of nocturnal terrestrial invertebrates.

Thompson, J. L. Cloudsley- (1958). The effect of wind upon the nocturnal emergence of woodlice and other terrestrial arthropods—2. *Ent. Mon. Mag.* **94**, 184-185.

The effect of wind and relative humidity on activity has already been established; from these further observations minimum temperature is seen to exert a threshold effect below which there is no activity.

Thompson, J. L. Cloudsley- (1958). The effect of wind upon the nocturnal emergence of woodlice and other terrestrial arthropods—3. *Ent. Mon. Mag.* **94**, 283-284.

These further observations were made at Appleton-le-Moors, Yorkshire. Activity of woodlice appears to be markedly reduced if surfaces are very wet.

Varley, G. C. & Gradwell, G. R. (1958). Oak defoliators in England. *Proc. 10th Int. Congr. Ent., Montreal*, 1956, **4**, 133-136.

The results of a 7 year study of *Operophtera brumata* and *Tortrix viridana* shows that parasitism is not high. Quantitative estimates of a parasite (*Cyzenis albicans*) show that the puparia suffer heavy mortality and synchronization is difficult. The efficiency of the specific parasites appears to be the major factor in determining whether a species can reach destructive abundance or not, but the timing of the outbreaks may be affected by the weather.

Wallace, H. R. (1958). Movement of eelworms. III. The relationship between eelworm length, activity and mobility. *Ann. Appl. Biol.* **46**, 662-668.

A study, based on the plotted tracks of about 300 eelworms of six species, on the relationship between mobility and soil particle size. Only among small particles is eelworm speed influenced by the size of the particles.

Williamson, K. (1958). Population and breeding environment of the St. Kilda and Fair Isle wrens. *Brit. Birds*, **51**, 369-393.

St. Kilda had about 230 pairs of *Troglodytes t. hirtensis* in 1957. Of 116 pairs on Hirta, 85% inhabit cliffs, especially puffinries, the remainder inland sites including the deserted village. Fair Isle had at most 50 pairs of *T. t. fridariensis* confined to the coast, chiefly narrow inlets with small beaches having wrack. Food preferences may control habitat selection, and *fridariensis* may be too specialized to colonize crofts.

Winfield, A. W. & Gough, H. C. (1959). Pests of mustard seed crops. *Agriculture*, **65,** 554-558.
Spraying to control pollen beetle and seed and stem weevils is discussed.

Worms, C. G. M. de (1958). The northward movement of certain species of European Lepidoptera and its relationship to climatic changes and other factors with special reference to the British Isles. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **1,** 737-740.
Discusses some twenty species which are classified into two groups; species which have become new colonizers and species of sporadic occurrence.

2. METHODS, APPARATUS, POPULATION STATISTICS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Andrewartha, H. G. (1957). The use of conceptual models in population ecology. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 219-236.
By relation to observations of animals in natural conditions, examines deterministic models based on the assumption that biotic factors are usually density dependent, and physical factors density independent.

Andrewartha, H. G. (1959). Density-dependent factors in ecology. *Nature, Lond.* **183,** 200.
Disputes the value of the concept of density-dependent factors in ecological work.

Askew, R. R. (1959). A revision of the genus *Olynx* Förster (Hym., Eulophidae). *Ent. Mon. Mag.* **95,** 49-57.

Bancroft, T. A. & Brindley, T. A. (1958). Methods for estimation of size of corn borer populations. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 1003-1014.
A method is described to illustrate the use of nested sampling designs for the efficient estimation of the mean and variance of a population. This method, involving optimum allocation, is extended to include the case of multiple available estimates of variance components.

Bliss, C. I. & Owen, A. R. G. (1958). Negative binomial distributions with a common *k*. *Biometrika,* **45,** 37-58.

Bliss, C. I. (1958). The analysis of insect counts as negative binomial distributions. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 1015-1032.
Two models are described and illustrated with entomological data. Two methods are used to fit a common index of dispersion to a related series of distributions with varying means.

Brass, W. (1958). Simplified methods of fitting the truncated negative binomial distribution. *Biometrika,* **45,** 59-68.

Brindle, A. (1958). Notes on the identification of *Limnophila* larvae (Diptera-Tipulidae). *Trans. Soc. Brit. Ent.* **13** (4), 57-68.
Key to species.

Brindle, A. (1958). Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 1—The larvae of *Tipula fascipennis* Mg. and *T. pagana* Mg., *Ent. Mon. Mag.* **94,** 230-232. Id. Part 2—The larvae of the subgenus *Vestiplex* Bezzi. *Ibid.*, **94,** 241-244. Id. Part 3—The larvae of *Tipula montium* Egg. and *T. couckei* Tonn. *Ibid.*, **94,** 272-274.

Brindle, A. (1959). Notes on the larvae of the British Tipulinae (Dipt., Tipulidae). Part 4—The larvae of *Tipula luteipennis* Mg. and *T. melanoceros* Schum. *Ent. Mon. Mag.* **95,** 36-37.
The larvae are described and keys to the different species given.

Claridge, M. F. (1958). The British and Scandinavian species of the genus *Cheiloneurus* Westwood (Hym., Encyrtidae). *Ent. Mon. Mag.* **94,** 156-161.
A revised key to the British and Scandinavian species of the genus.

Claridge, M. F. (1959). A contribution to the biology and taxonomy of the British species of the genus *Eudecatoma* Ashmead (— *Decatoma* auctt. nec Spinola) (Hym., Eurytomidae). *Trans. Soc. Brit. Ent.* **13** (9), 149-168.

Claridge, M. F. (1959). The identity of *Eurytoma appendigaster* (Swederus, 1795) (Hym., Eurytomidae), together with descriptions of some closely allied species bred from Graminae. *Ent. Mon. Mag.* **95,** 2-13.

Cole, L. C. (1957). Sketches of general and comparative demography. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 1-15.
General discussion of terminology, comparisons of life histories, population regulation, age structure, etc.

Cole, L. C. (1958). Population fluctuations. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 639-647.
The simple assumption that population size tends to fluctuate at random, but under some influence from past history as well as present events, predicts 'population cycles' very similar to those observed in nature.

Collin, J. E. (1958). A short synopsis of the British Scatophagidae (Diptera). *Trans. Soc. Brit. Ent.* **13** (3), 37-56.
Keys to genera and species.

Collingwood, C. A. (1957). The species of ants of the genus *Lasius* in Britain. *J. Soc. Brit. Ent.* **5,** 204-214.
Gives a key to species and notes on distribution.

Crow, E. L. (1958). The mean deviation of the Poisson distribution. *Biometrika,* **45,** 556-559.

Darroch, J. N. (1958). The multiple-recapture census. 1. Estimation of a closed population. *Biometrika,* **45,** 343-359.
Discusses the theory of marking for cases where recaptured marked individuals can again be released for further recapture.

Eady, R. D. (1958). A revision of the nomenclature in the European Torymidae (Hym., Chalcidoidea) with special reference to the Walker types. *Ent. Mon. Mag.* **94,** 257-271.

Gillies, M. T. (1958). A simple autoradiographic method for distinguishing insects labelled with phosphorus-32 and sulphur-35. *Nature, Lond.* **182,** 1683-1684.
Based on the differences in the energy of the radiations from the isotopes. Insects can be separated on exposure to X-ray film laid in two superimposed layers. No radiation from ^{35}S reaches second layer.

Goodliffe, F. D. (1958). Elytral characters and sexual dimorphism in a Surrey population of *Agabus melanarius* Aubé (Coleoptera: Dytiscidae). *Proc. R. Ent. Soc. Lond. (A),* **33,** 196-200.
Describes a simple method of (*a*) recognizing specimens in the field and (*b*) drawing and measuring elytral sculpture. A wide range of variation in the degree of elongation of the major elytral reticulation in the discal region is reported from this apparently unique population.

Graham, M. W. R. de V. (1959). Notes on Pteromalidae (Hym., Chalcidoidea), with descriptions of new genera and species. *Trans. Soc. Brit. Ent.* **13** (6), 97-112.

Graham, M. W. R. de V. (1959). Keys to the British genera and species of Elachertinae, Eulophinae, Entedontinae, and Euderinae (Hym., Chalcidoidea). *Trans. Soc. Brit. Ent.* **13** (10) 169-204.

Hickin, N. E. (1958). Larvae of the British Trichoptera: 52. *Proc. R. Ent. Soc. Lond.* (*A*), **33,** 176-178.
The larva of *Enoicyla pusilla* is described and figured.

Hincks, W. D. (1957). Notes on some species of Trichogrammatidae (Hym., Chalcidoidea) omitted from the 'Check list of British Insects'. *J. Soc. Brit. Ent.* **5,** 215-218.

Hincks, W. D. (1959). The British species of the genus *Alaptus* Haliday *in* Walker (Hym., Chalc., Mymaridae). *Trans. Soc. Brit. Ent.* **13** (8), 137-148.

Huffaker, C. B. (1958). The concept of balance in nature. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 625-636.
A general review of the recent literature on the dynamics of animal populations which attempts to state the differences and the agreement between the leading theorists.

Laughlin, R. (1958). The rearing of crane flies (Tipulidae). *Ent. Exp. Appl.* **1,** 241-245.
Eggs incubated on damp filter paper, larvae reared in damp drained sand, fed on powdered dried grass, pupae kept in damp blocks of plaster of paris.

Leatherdale, D. (1958). A host catalogue of British entomogenous fungi. *Ent. Mon. Mag.* **94,** 103-105.

Leslie, P. H. (1958). A stochastic model for studying the properties of certain biological systems by numerical methods. *Biometrika,* **45,** 16-31.
Theoretical models for growth of a species in a limited environment, of two species competing and a predator/prey system. With applications to Gause's (1934) data for *Paramecium* populations.

Leslie, P. H. & Gower, J. C. (1958). The properties of a stochastic model for two competing species. *Biometrika,* **45,** 316-330.

Love, S. K. & Thatcher, L. L. (1957). Water analysis. *Analyt. Chem.* **29,** 722-734.
Reviews work published in 1955 and 1956 on water analysis, with bibliography.

McGuire, J. U. (1958). The use of the range from Poisson populations to estimate the population variance. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 1033-1036.
Shows that the approximation to the variance of a Poisson distribution by means of the range and Tippett's table will be useful for distributions with means of four or above and for sample sizes from two to eight.

McGuire, J. U. & Wirth, W. W. (1958). The discriminant function in taxonomic research. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **1,** 387-393.
Describes the use of discriminant functions to test the validity of five subspecies of *Culicoides variipennis,* three being well defined, one intermediate and one indistinguishable. The technique for computing the discriminant functions is explained.

Martin, D. L. (1959). Self-regulation in living systems. *Nature, Lond.* **183,** 370.
An account of a symposium. Non-oscillatory state in animal populations deemed optimum condition for survival. Some animals contribute to stable state by relatively inefficient breeding habits in combination with tendencies to high death rate. Analogy is drawn to feedback system characteristics. Some ecological systems show an apparent ability to 'learn'.

Milne, A. (1957). The natural control of insect populations. *Canad. Ent.* **89,** 193-213.
Discusses current theories of population control and propounds that control is the resultant of combined density independent and imperfectly density dependent factors, each supplying the lack of the other. Ultimate control of decrease of numbers is by density independent factors.

Milne, A. (1957). Theories of natural control of insect populations. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 253-271.

Reasserts the theory put forward in *Canad. Ent.* **89,** 193-213 (noted above). Discussion by the symposium is appended.

Milne, A. & Solomon, M. E. (1958). Perfect and imperfect density-dependence in population dynamics. *Nature, Lond.* **182,** 1251-1252.

Milne postulates that intraspecific competition is the only perfect d.d. factor, whilst interspecific competition is imperfect. He suggests there is no advantage in adopting Solomon's classification of d.d. factors (see *Nature, Lond.* **181,** 1778). Solomon defends his views.

Muir, R. C. (1958). On the application of capture-recapture method to an orchard population of *Blepharidopterus angulatus* (Fall.) (Hemiptera-Heteroptera, Miridae) *Rep. East Malling Res. Stn.,* **A41,** 140-147.

The method of marking is described and the marking programme outlined. The data are analysed to examine the influence of sex, age and recapture on survival. Estimates of population, daily dilution and wastage rates were obtained by a new method of analysis devised by G. M. Jolly.

Neyman, J. & Scott, E. L. (1957). On a mathematical theory of populations conceived as conglomerations of clusters. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 109-120.

Stochastic models relating to distribution, behaviour, size, dispersal and survival of litters.

Nye, I. W. B. (1958). The external morphology of some of the dipterous larvae living in the Graminae of Britain. *Trans. R. Ent. Soc. Lond.* **110,** 411-487.

Includes a key to the third instar larvae of forty-one species belonging to the Pallopteridae, Anthomyzidae, Opomyzidae, Ephydridae, Chloropidae, Cordiluridae and Muscidae.

Perkins, J. F. (1958). A new genus and three new species of Polysphinctini from Europe (Hym. Ichneumonidae). *Entomologist,* **91,** 263-267.

These include *Piogaster albina,* recorded from Norfolk and *P. punctulata* from Surrey.

Ramasubban, T. A. (1958). The mean difference and the mean deviation of some discontinuous distributions. *Biometrika,* **45,** 549-556.

Schwerdtfeger, F. (1958). Is the density of animal populations regulated by mechanisms or by chance? *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **4,** 115-122.

Postulates that in many cases random influences (*e.g.* weather factors) have an essential or decisive effect both on immediate abundance and on long-term population changes and that these random factors can maintain populations at stable levels. Model experiments and reference to population fluctuations of three forest insects in Germany from 1881 to 1940 are used to support this contention.

Scudder, G. G. E. (1958). On *Salda morio* Zett. and *S. muelleri* (Gmel.) (Hem., Saldidae) in Britain. *Ent. Mon. Mag.* **94,** 190-191.

A key and description of the two species. *S. morio* is a northern form; *S. muelleri* is found in southern districts.

Skellam, J. G. (1958). On the derivation and applicability of Neyman's type A distribution. *Biometrika,* **45,** 32-36.

Discusses the application to other situations of a method particularly suited to sampling organisms occurring in compact clusters.

Sokal, R. R. (1958). Quantification of systematic relationships and of phylogenetic trends. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **1,** 409-415.

Three methods (partial correlations, factor analysis and principal components) are described, with examples, to determine the interrelationships of systematic entities.

Steel, W. O. (1958). Notes on the Omaliinae (Col., Staphylinidae). *Ent. Mon. Mag.* **94,** 138-142.

Descriptions of five species of the genus *Micralymma* Westwood with a key to the species.

Surtees, G. (1959). Influence of larval population density on fluctuation in mosquito numbers. *Nature, Lond.* **183,** 269-270.

Concludes that fluctuations of *Aedes aegyptii* depend upon larval density, not on climatic conditions.

Swennen, C. & Baan, G. van der (1959). Tracking birds on tidal flats and beaches. *Brit. Birds,* **52,** 15-18.

Descriptive notes on photographs of marks left by birds and the holes of some prey species of marine worms.

Tarshis, I. B. (1958). Feeding techniques for bloodsucking arthropods. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **3,** 767-784.

An apparatus and technique are described for the *in vitro* feeding of fleas, mosquitoes and ticks.

Utida, S. (1957). Population fluctuation, an experimental and theoretical approach. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 139-151.

Discusses fluctuation of population under constant environmental conditions relative to (1) a single species population, (2) a host parasite system, (3) a system with two species of parasite attacking their host.

Varley, G. C. & Gradwell, G. R. (1958). Balance in insect populations. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 619-624.

Observations on the fluctuations of oak defoliators and their parasites suggest that the mathematical formulation of Nicholson and Bailey overlooks protective mechanisms, these tending to reduce the violence of the population oscillations. Niches, parasite restraint, temporal changes and spatial differences are quoted as examples.

Varley, G. C. & Nicholson, A. J. (1959). Density-dependent factors in ecology. *Nature, Lond.* **183.**

Criticisms of Andrewartha's (see *Nature, Lond.* **813,** 200) ideas on density-dependency. Varley discusses the validity of population models of Lotka and Volterra, Nicholson's equation representing the conditions necessary for population equilibrium in a postulated simple situation, and the design of experiments to test the action of density-dependent factors.

Voûte, A. D. (1958). On the regulation of insect populations. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **4,** 109-114.

In a general review of the factors which regulate insect populations it is shown that parasites will regulate hosts at fixed levels only when in combination with density-dependent factors which will 'quench' the oscillations—with ever-increasing amplitude otherwise inherent in the host-parasite relationship. Discusses and classifies the 'quenching' principle in relation to the biological control of insect pests.

Wangersky, P. J. & Cunningham, P. J. (1957). Time lag in population models. *Cold Spr. Harb. Symp. Quant. Biol.* **22,** 329-338.

Single species growth curves, prey-predator growth curve and interspecies competition.

Wilson, D. P. (1958). The polychaete *Magelona alleni* n.sp. and a re-assessment of *Magelona cincta* Ehlers. *J. Mar. Biol. Ass. U.K.* **37,** 617-626.

3. PARASITES

Badami, R. S. (1958). Changes in the transmissibility by aphids of a strain of cucumber mosaic virus. *Ann. Appl. Biol.* **46,** 554-562.

A study of differential virus transmission rates by the aphids *Myzus persicae, M. circumflexus, M. ascalonicus* and *Aphis gossypii,* and of the transmission of different strains of the same virus.

Bailey, R. (1957). Observations on the size of galls formed on couch grass by a chalcidoid of the genus *Harmolita* Motschulsky (*Isosoma* Walker) Hym. (Eurytomidae). *J. Soc. Brit. Ent.* **5,** 199-203.

Galls formed on *Agropyron repens* show a bimodal size distribution. Sexual dimorphism in the larvae occurs, the females being larger and initiating the development of larger galls.

Bailey, R. (1959). Facultative parasitism and dietary change in *Harmolita hyalipenne* Walker. *Nature, Lond.* **183,** 341-342.

Describes the ecological relationship between *Harmolita graminicola* and *H. hyalipenne* in couch grass. The eggs of the former are laid close to the young galls. On hatching they give rise to active grubs which attack and destroy the gallicolous larvae of *H. graminicola*. This parasitism, however, is shown to be facultative, and the grubs may form typical galls.

Becker, P. (1958). Some parasites and predators of biting midges, *Culicoides* Latreille (Dipt., Ceratopogonidae). *Ent. Mon. Mag.* **94,** 186-189.

Nereis diversicolor is probably a regular predator of *Culicoides* larvae. Parasites of the midges included species of bacteria, ciliata and acarina.

Burnett, T. (1958). A model of host-parasite interaction. *Proc. 10th Int. Congr. Ent., Montreal,* 1956, **2,** 679-686.

A study of *Trialeurodes vaporariorum* and its parasite *Encarsia formosa* over twenty-one generations in the laboratory shows that the population changes generally follow those calculated from the equations of Nicholson and Bailey.

Jackson, D. J. (1958). Observations on the biology of *Caraphractus cinctus* Walker (Hymenoptera: Mymaridae), a parasitoid of the eggs of Dytiscidae. I. Methods of rearing and numbers bred on different host eggs. *Trans. R. Ent. Soc. Lond.* **110,** 533-554.

Gives details of the distribution of this parasitoid in Britain, technique and methods of rearing from various Dytiscidae, behaviour and life history. Discusses superparasitism and its effect on sex ratio.

Jackson, D. J. (1958). Notes on some Nematodes and Trematodes infesting water beetles. *Ent. Mon. Mag.* **94,** 109-111.

Identification and description of Nematode and Trematode eggs found on dissection of water beetles.

Jennings, A. R. (1959). Diseases of wild birds, fifth report. *Bird Study,* **6,** 19-22.

Of 247 birds examined post mortem between June 1957 and June 1958, fifty-four died of infectious disease, 111 by accident and poison. Dieldrin seed dressings poisoned many birds, particularly wood pigeons.

Slykhuis, J. T. & Watson, M. A. (1958). Striate mosaic of cereals in Europe and its transmission by *Delphacodes pellucida* (Fab.). *Ann. Appl. Biol.* **46,** 542-553.

Delphacodes pellucida was established as the vector of a virus disease on various graminaceous plants at Harpenden in 1956. The virus was transmitted through the eggs to as many as 88% of the progeny of infected females.

4. FOOD AND FOOD HABITS

Baker, C. S. Wood- (1958). The oviparous female of *Vesiculaphis theobaldi* Tak. and notes on its food plants. (Hem., Aphididae). *Ent. Mon. Mag.* **94,** 100-102.

An apterous female from colonies of *V. theobaldi* reared on *Carex remota* and *C. sylvatica* was seen laying eggs.

Crichton, M. I. (1959). Attacks by birds on caddis flies. *Bird Study,* **6,** 22-25.

Distinctive nicking, often of both wings, of caddis flies taken in a light trap near Reading suggests attack by birds when at rest.

Haggett, G. (1958). Larval food plants of some Noctuae. *Entomologist,* **91,** 267.

Larvae of five species have been found, sometimes consistently, on food-plants other than those usually attributed to them. They are *Lithacodia fasciana* on *Agrostis* sp. in Suffolk; *Euclidimera mi* on various grasses and *Phragmites*; *Heliophobus saponariae* on *Ononis* and other leguminous plants as well as *Silene* in the Breck; *Melanchra persicariae* on coniferous foliage; and *Heliothis maritima septentrionalis* on *Calluna* in the New Forest.

Hudleston, J. A. (1958). Some notes on the effects of bird predators on hopper bands of the desert locust (*Schistocerca gregaria* Forskål). *Ent. Mon. Mag.* **94,** 210-214.
A list of birds seen feeding on locust hoppers is given, and the general effect of bird predation on hopper groups discussed.

Hueck, H. J. (1958). The development of a comparative method for the evaluation of the moth-proofness of wool serge. *Ann. Appl. Biol.* **46,** 511-528.
Includes data on the weight losses of woollen serge from feeding by the common clothes moth (*Tineola bisselliella*).

Richards, T. J. (1958). Concealment and recovery of food by birds, with some relevant observations on squirrels. *Brit. Birds,* **51,** 497-508.
Food-storing habits of coal tit, marsh tit, nuthatch, jay and rook are described. Grey squirrels (*Sciurus carolinensis*) distribute buried food over their territories and recover it by scent. Of twenty-one items buried by the author between mid-October and December only four had not been removed by 31 January.

5. MIGRATION, INTRODUCTIONS AND LOCAL DISTRIBUTION

Aston, A. (1958). Additions to the Suffolk Lepidoptera. *Ent. Rec.* **70,** 306.
Dates and localities for nine of the forty-nine species added since the publication of the county list in 1937.

Baynes, E. S. A. (1958). Supplement to a list of the Lepidoptera of Tory Island, Co. Donegal. *Entomologist,* **91,** 207.
A list of nine additional species. (See 1957, *Entomologist,* **90,** 310 and abstract in 1959, *J. Anim. Ecol.* **28,** 182).

Brown, R. G. B., Ashmole, N. P. & Campbell, R. P. (1958). Insect migration in the Pyrenees in the autumn of 1955. *Ent. Mon. Mag.* **94,** 217-226.
A report of insects seen migrating in the Gavarnie area of the Hautes Pyrénées. A list of species collected is given and the effect of weather upon migration discussed. The stronger fliers appear to fly over the main ridge in favourable weather, and are forced into the lower passes only by head winds.

Elkin, Hazel W. (1955). Whiting (*Gadus merlangus* L.) in Irish waters. *Sci. Proc. Roy. Dub. Soc.* **27,** 17-30.
Comparative study of monthly samples of commercially caught whiting from the east and west coasts of Ireland taken over a period from November 1952 to June 1954.

Haggett, G. (1958). Rediscovery of the marsh carpet, *Perizoma sagittata* Fabricius, in Norfolk. *Entomologist,* **91,** 231-232.
This moth, regarded as possibly extinct, was rediscovered in 1954 and was plentiful in 1956. Its sporadic appearance may be associated with the varying success of its food-plant (*Thalictrum*), which has lately both spread and increased. The seed heads, on which the larva feeds, are often infested by mildew and a disease causes the flowers and upper parts of the stem to blacken. Spiders, earwigs and predaceous Hemiptera frequent the seed heads and probably cause considerable mortality among the eggs and young larvae.

Healy, Ann (1956). Pike (*Esox lucius* L.) in three Irish lakes. *Sci. Proc. Roy. Dub. Soc.* **27,** 51-63.
A comparative survey of the spawning times, growth rates, sex ratios and feeding habits of pike taken from Lough Glore, Lough Rea and Barnagrow lake in the years 1950-4.

Hollom, P. A. D. (1959). The great crested grebe sample census 1946-1955. *Bird Study,* **6,** 1-7.
A consolidated report for the period indicated and comparison with data from previous censuses. After an increase in 1953 and 1954 to nearly 150% of 1931 populations, the figure fell to 131% in 1955. Distribution within Britain is discussed.

Jacob, F. H. & Janson, H. W. (1958). Colorado beetle. *Agriculture*, **65,** 393-397.
No breeding colony was reported in 1957, but forty-eight individual beetles were discovered as compared with fifty-one in 1956 and fifty-four in 1955.

Johnson, A. L. (1959). Seal marking—1958. *Nature in Wales*, **5,** 717-724.
One hundred and fifty-one seals were marked with numbered metal toe-rings in West Wales during 1958, most of them on Ramsey Island; of which six were recovered locally and five in other areas.

Jones, S. B. & Jones, P. E. H. (1959). Crowned cranes in Cambridgeshire. *Nature, Lond.* **183,** 560.
Four birds observed. Descriptions given.

Kisch, B. S. (1959). *Balanus tulipiformis* Ellis on the Atlantic coast of France. *Nature, Lond.* **183,** 341.
Re-identification of material shows that this barnacle was first found on this coast 25 years ago.

McMillan, N. F. (1959). The Mollusca of some Cheshire marl-pits: a study in colonization. *J. Conch.* **24,** 299-314.
A survey extending over several years of the freshwater Mollusca of 172 ponds in old marl-pits in the Wirral peninsula, chiefly from the dispersal aspect and the ecological requirements of the Mollusca.

Michaelis, H. N. (1958). *Gelechia boreella* Douglas in England. *Ent. Rec.* **70,** 305.
This moth, apparently known hitherto only from the Scottish Highlands, was plentiful at the end of July in 1956 and 1958 among long grass bordering marshy ground and sheltered by birch, alder and sallow bushes at about 1100-1200 ft. in north-west Yorkshire.

Sage, B. L. (1959). Notes on dragonflies in Wales in 1958. *Nature in Wales*, **4,** 729-732.
Although numbers were at a low ebb owing to the bad summer, six new county records are noted; *Ceriagrion tenellum* and *Orthetrum coerulescens* from Cardiganshire, *Aeshna juncea* from Radnorshire, and *Anax imperator* and *Ischnura pumilio* from Breconshire.

Southward, A. J., Southward, E. C. & Cooper, L. H. N. (1958). On the occurrence and behaviour of two little-known barnacles, *Hexelasma hirsutum* and *Verruca recta*, from the continental slope. *J. Mar. Biol. Ass. U.K.* **37,** 633-647.
Descriptions and analysis of laboratory behaviour in relation to natural habitat.

6. STUDIES ON BEHAVIOUR

Armstrong, E. A. (1959). Display by swifts. *Brit. Birds*, **52,** 97.
A swift followed another at about 20-25 ft above the ground. The leading bird was swooping towards overhanging house gutters, the other repeating its movements, for several minutes. The movements appeared appropriate for nest-site selection, but there was no suitable site.

Betts, M. M. (1958). The behaviour of adult tits towards other birds and mammals near the nest. *Brit. Birds*, **51,** 426-429.
Other small passerines were ignored but predators interrupted feeding visits, and tits reacted differently to a sparrowhawk than other birds. A female great tit crouched on her nest and displayed when attacked by a great spotted woodpecker. A male great tit displayed and flew at a red squirrel (*Sciurus vulgaris*) near its nest, but the female continued to visit it.

Hulme, D. C. (1959). Breeding season calls of the chaffinch and greenfinch. *Brit. Birds*, **52,** 83-85.
Twelve years' records show that the 'chwit' call of the chaffinch extends over 3, the 'tsweee' call of the greenfinch over 6 months, and the calls may be substitutes for full song.

King, M. Brooks- & Hurrell, H. G. (1958). Intelligence tests with tits. *Brit. Birds*, **51,** 514-524.
Apparatus used in tests is described and illustrated. Birds of the same species show individuality in solving tests, and the aptitude of different species varies.

Salmon, H. M. (1958). Lesser black-backed and herring gulls nesting on a factory roof inland in Glamorgan. *Brit. Birds,* **51,** 399-401.

The colony has gradually increased since 1945 or 1946, and in 1958 had about 120 birds with twenty-six occupied nests of lesser black-backed and nineteen of herring gulls. On an asbestos sheeting roof at Merthyr Tydfil.

Thorpe, W. H. & Pilcher, P. M. (1958). The nature and characteristics of sub-song. *Brit. Birds,* **51,** 509-514.

Sub-song is defined. It is usually produced early in the season, and may be a form of 'practice' for full song, especially in young birds.

Vernon, J. D. R. & Avent, C. (1959). Lesser black-backed gull nesting on a bush. *Brit. Birds,* **52,** 60.

The nest was on a privet bush 3 ft above the ground, on Steep Holm in the Bristol Channel. The gulls habitually perched on the bushes, and nested on the ground among them.

Wilson, D. R. (1959). Display of little grebe. *Brit. Birds,* **52,** 96.

The display, a form of penguin-dance, aroused no response in the bird at which it was directed.

BRITISH ECOLOGICAL SOCIETY

WINTER AND ANNUAL GENERAL MEETING

2 AND 3 JANUARY 1959

The Winter Meeting, 1959, was held at Oxford in the Department of Zoology and Comparative Anatomy. Professor Sir Alister Hardy welcomed some 100 members at the start of the meeting at 2.15 p.m. on 2 January, and the programme commenced with a paper by Miss K. Paviour-Smith on 'The insect inhabitants of the birch-bracket fungus'.

Forty-two species of insects, most of them beetles, have been recorded from *Polyporus betulinus* in Britain. Miss Paviour-Smith said that she had found at least twenty-seven species of invertebrates, again mostly beetles, associated with this fungus, in three or more of fifty-six localities examined. The commonest species everywhere in live brackets was *Tetratoma fungorum*, and in southern Britain in dead brackets *Cis bilamellatus*.

The speaker described a quantitative seasonal study on brackets in Wytham Woods, Berks., to observe the timing of this succession. The life history of *Tetratoma fungorum* was outlined, and also the habitat components which it requires besides its fungus food. Eleven trees were 'age-ranked' by three independent methods to find why populations attain vastly different densities on different trees. They fell into two main groups—'good' or 'poor' *T. fungorum* habitats—depending on whether or not all the necessary habitat components were present and well interspersed.

Cis bilamellatus populations were followed for their first year from colonization in two newly dead brackets, and for their second year in a bracket which was a year older. The spread of this Australian species in Britain, since 1884, and its present distribution were described.

The paper was followed by questions from Professor O. W. Richards, Dr D. J. Crisp, Mr N. Wace and Dr F. Raw. Miss Paviour-Smith stated that effective destruction of the fungus takes place only with an exceptionally great infestation by beetles.

Contributions from Professor W. T. Williams ('Association-analysis: an objective method for the analysis of vegetation by an electronic computer') and Dr J. M. Lambert ('The ecological implications of association-analysis'), followed consecutively. Professor Williams presented the view that the basic problem of primary survey is to establish boundaries; the function of association-analysis is to provide an objective method of finding such boundaries, even if the ecological behaviour of the species in question is unknown. The method derives from two sources: first, the postulate by Nordhagen (1928) that associations between species in an area are evidence of heterogeneity; and secondly, the statement by Goodall (1953) that a group of quadrats showing such associations can be divided into 'homogeneous' groups, in which all species-associations have been made indeterminate (a given species being present or absent in all quadrats of the group) or have fallen below a predetermined level of significance. Correlation coefficients between all possible pairs of species are calculated from a set of 2×2 contingency tables, and the coefficients relating to each species are summed regardless of sign; it can be shown that division of the population on the species with the highest sum is the most efficient which can be obtained by simple means. The resulting sub-populations are similarly subdivided until all resulting groups are free from associations with less than an assigned value of χ^2 (with Yates's correction), the entire process being carried out automatically by a 'Pegasus' digital computer. The boundaries of the final groups so obtained are plotted on a map.

Dr Lambert discussed four examples of the application of association-analysis to specific areas of vegetation, three from gridded rectangles of heathland in the New Forest, containing six, seventeen and thirty-three vascular species respectively, the fourth from scattered quadrats in the Rockland-Claxton Level in Norfolk, with seventy-two species. In each case, the boundaries of the quadrat groupings could be related to recognizable features of the habitat, and in three of the areas the analysis drew

attention to important ecological factors which had previously been overlooked. The first example consisted of heathland divided into strips which had been accidentally burnt at varying times; but the major division of the analysis revealed a hidden geological boundary as more important than the burning pattern, which only appeared at the second stage. The second area lay over a similar geological boundary and was bisected longitudinally by a recent burning line; but here the analysis picked out the presence of former cart-tracks and an unsuspected older burning as the major factors in the area, and ignored the soil transition and the recent burning. In both these examples, further consideration showed that the analysis had given a better ecological picture than the initial assessment. In the third area, however, which was specifically selected as showing an exceptionally clear and regular zonation from dry heath to bog, the analysis reiterated the original picture, and retained the zoning at all levels.

The Rockland-Claxton data had already been published and analysed subjectively in terms of relative distribution of peat and clay and of differences in mowing and grazing intensity. The five major groupings of the objective analysis retained some suggestion of the peat/clay relationship, but ignored the current grazing pattern in favour of a very clear boundary related to historical differences in time of drainage. Furthermore, one of the divisions exposed inconsistencies in the original collection of the data by different pairs of students.

In the general discussion on these two papers, to which Mr N. Wace, Professor A. R. Clapham, Dr F. Raw, Professor D. A. Webb, Mr P. Greig-Smith and Mr J. G. Skellam contributed, the question was raised of the possibility of extending the analysis beyond the 'presence or absence' type of data to quantitative measures of the occurrence of species in quadrats. Mr Greig-Smith, pointing out that the boundary beyond which a species is absent represents only the end of a zone of falling-off in contribution to the community, suggested that the method would over-emphasize the sharpness of boundaries. However, Professor Williams pressed his claim that his method reveals the positions of the greatest floristic discontinuities in the field, thus opening up the most significant lines for ecological inquiry.

The next paper, by Mr P. Jewell, concerned 'The small vertebrate fauna of Salisbury Plain in Bronze Age times'.

During the summer of 1957 the excavation of Bronze Age barrows at Snail Down on Salisbury Plain yielded a number of aggregates of small bones. These bones were sealed in at the level of the old land surface and were the remains of the pellets disgorged by some raptorial bird. Stake holes found in the chalk rock under the barrows suggested that the birds had been attracted to these particular sites by the perching-places offered by stakes.

The bones recovered are mostly those of small mammals, namely the mole (*Talpa europea*), the water vole (*Arvicola amphibius*), the short-tailed vole (*Microtus agrestis*), the wood mouse (*Apodemus sylvaticus*), the common shrew (*Sorex araneus*), and the pigmy shrew (*S. minutus*). Live-trapping round the barrows with Longworth traps showed that the short-tailed vole, the wood mouse and the common shrew are present locally today. The absence of the bank vole (*Clethrionomys glareolus*) from both the traps and the Bronze Age pellets is noteworthy. In addition to the mammals the toad (*Bufo bufo*) was a common item of prey, and the osteoderms of the slow worm (*Anguis fragilis*) were numerous. Lizard was present but the species could not be identified from the fragmentary remains. Remains of small birds were rare but the skylark (*Alauda arvensis*) and the corn-bunting (*Emberiza calandra*) could be identified.

The numerous water vole bones were examined in detail. No feature could be found to distinguish the remains from those of modern *Arvicola amphibius*. An abundance of this typically waterside animal on a free-draining chalk upland invites speculation. In the absence of any evidence for a wetter climate or higher water table in Bronze Age times it seems most likely that the water vole was occupying a wider range of habitats than now. The absence of the rabbit and both brown and black rats may have been important factors allowing this extended distribution.

An examination of the molar teeth of the *Microtus agrestis* remains gave some indications that the Bronze Age population was similar to the modern Highland form (*M. a*

neglectus) and differed from the southern British form (*M. a. hirtus*). The ascendancy in the south of the subspecies *M. a. hirtus* may thus be a recent phenomenon.

The paper, noteworthy also for the quality and attractiveness of the colour illustrations of the finds referred to, was discussed by Professor G. C. Varley, Mr H. N. Southern, Dr M. Ashby, Mr E. D. Le Cren, Mr E. J. Moynahan and Mr J. G. Skellam.

Concluding the afternoon's programme, Dr D. Nichols spoke on 'Ecological problems concerning extinct sea-urchins'.

The complex series from the English Chalk of fossil heart-urchins of the genus *Micraster* shows both a continuous, directional variation of individual characters with time and a range of variation at any one stratigraphical horizon. Some of the most conspicuous features which change concern the ornamentation of those parts of the test which gave rise to the tube-feet in life, features which are important in field stratigraphy. In attempting to elucidate the change in niche which these variations represent, use has been made of the fact that comparable ornamentation exists in closely related living forms. For instance, the areas of the test of the recent *Echinocardium cordatum* to which are attached extensile tube-feet whose activity is always perpendicular to the test surface, *e.g.* the dorsal funnel-building tube-feet are small compared with those bearing tube-feet which move at all angles to the test, such as the oral feeding tube-feet. This reflects the fact that the bases of tube-feet moving at all angles must be broader than those moving at right-angles only, to obtain the necessary leverage for such movement. Similar attachment areas can be seen on the test of *Micraster*, and this enables a comparison of tube-foot activity in relation to the test to be made both for different regions of the same specimen and for different specimens which vary in this character. Evidence of this sort has shown that the early, 'low-zonal' forms burrowed less deeply in the substratum than 'high-zonal' forms. At the top of the *planus* zone of the Middle Chalk the shallow-burrowers, *M. corbovis*, die out, and soon after this another form, *M.* (*Isomicraster*) *senonensis*, appears probably by immigration. The latter is not sufficiently distinct from the main *Micraster* line to prevent interbreeding with it. From its shape and the ornamentation of its pores it is probable that this form burrowed even shallower in the silt than *M. corbovis*, with part of its corona exposed above the surface. It thus seems likely that *M. senonensis* took over a niche left vacant after the failure of *M. corbovis*.

Questions were asked by Dr D. J. Crisp and Professor G. C. Varley.

An informal dinner was held in the evening in Jesus College, followed by a soirée in the Department of Zoology and Comparative Anatomy where a number of exhibits were on view. These included several which related to papers being delivered during the meeting. Miss K. Paviour-Smith demonstrated *Tetratoma fungorum* and *Cis bilamellatus*; Professor W. T. Williams showed examples of the preparation of data and the methods of programming for analysis of quadrat records by an electronic computer; Dr D. Nichols presented an exhibit on evolution in *Micraster*; illustrations of the results of studies on population dynamics of the first generation of *Erioischia brassicae* Bouché (Diptera; Anthomyidae) were shown by Dr R. D. Hughes; and the soil oxygen diffusion meter used by Dr L. W. Poel was on view. In addition there were exhibits of an ecological study of Winter Moth and other defoliators by Professor G. C. Varley, and the life history pattern of two closely related Psocid species and of their common Mymarid parasite by Dr E. Broadhead.

On Saturday morning, 3 January, the Annual General Meeting (see below) was followed by Professor N. A. Burges's Presidential Address 'Time and size as factors in ecology'. This address will be printed in full in both of the Society's Journals.

The final session, after lunch, was devoted to four papers. In the first, Dr R. D. Hughes considered 'The natural mortality of *Erioischia brassicae* (Diptera; Anthomyidae) during the egg stage'. He quoted evidence indicating predation of the eggs on brassica crops at Wellesbourne, Warwickshire, by the ground beetle fauna. When counts are made of the number of eggs laid, this predation results in an underestimate of the total. However, a method was devised for deriving the average survival of eggs, over a short period of time, by counting them at different time intervals. Dr Hughes showed that predation losses over the short periods could be related to daily trap-catches of predators over the same periods. This relationship of predation to the daily trap-catch of beetles was used

to estimate the probability of egg survival on each day. From the latter, in conjunction with the number of eggs counted, an estimate could be made of the total number of eggs laid. Calculations showed that egg predation is the major cause of egg mortality, accounting for over 90% of the losses in the 1957 and 1958 first generations of *E. brassicae*. The role of the weather in modifying predation efficiency was also discussed.

A number of points were raised in discussion, including the question of the degree to which high egg mortality controls the population of adults. Dr Hughes's view was that variations in the populations of surviving adults depend more on this factor than any other. Taking part were Mr J. G. Skellam, Mr M. E. Solomon, Professor G. C. Varley, Mr E. D. Le Cren, Mr G. A. Gardwell, Professor O. W. Richards and Dr F. Raw.

Dr J. Warren Wilson, in a paper on 'Analysis of the spatial arrangement of foliage by two-dimensional and inclined point quadrats', said that the point quadrat method has two serious faults. (i) Because the needles are not true points the area of foliage is overestimated, often by more than 50%; this error can be avoided by recording foliage contacts with only the point (not the side) of an advancing needle. (ii) Because the method estimates the area of foliage in vertical projection it underestimates the true area to an extent depending on the slope of the foliage; however, a combination (in appropriate proportions) of the numbers of contacts made by quadrats inclined at certain angles to the ground gives accurately the true area of foliage per unit area of ground. This is a more realistic measure of the effective quantity of vegetation than are traditional quantitative ecological measures, and it can be directly related to physiological results. Also, this extension of the point quadrat method can estimate distribution of foliage area with height above ground, angle of inclination of foliage, and foliage dispersion; these features affect light penetration, and hence growth and competition.

Among those questioning the speaker were Dr M. Ashby and Dr E. W. Jones.

Mr R. Moreau's paper on 'The avifaunas of four archipelagos' dealt with the following regions:

The Balearics are quasi-continental, isolated from Spain successively since the late Pliocene. Majorca, the biggest island, has also more mountain and marsh than the other three. The avifauna of the archipelago as a whole is a depauperate form of the eastern Spanish; each island has a shorter list of breeding birds than the next largest, but Ibiza has unaccountably few.

The Canaries, oceanic and volcanic, vary in climate from desert in the two eastern to marine in the western; and all but the two eastern are mountainous. Except for Saharan elements on these two the avifauna is palaearctic, presumably from invaders during a glaciation. Some species have been shown to have more extensive ecological niches than on the continent.

The Gulf of Guinea islands. Fernando Po, the biggest, is continental, the other three oceanic. They all retain humid forest, and their birds must have been derived from the neighbouring forested mainland. In the oceanic islands a quarter of the species are endemics and include exceptionally large members of several families.

The East African islands. Pemba, Zanzibar and Mafia are all within 25 miles of Africa, flat, humid and with only small forest remnants. But the water isolating the last two from the mainland is very shallow while the Pemba channel is deep and presumably of different history. All three avifaunas are depauperate versions of that of the mainland coast, while Pemba in particular lacks some of the most important families.

Mr Moreau showed that with very few exceptions, in each archipelago the numbers of resident birds per island are in the same order as the sizes of the islands, but the numbers by no means increase proportionately with the sizes. Three of the four exceptional avifaunas are explicable on peculiarities of the environment or the geological history. Endemism varies closely in accord with history of isolation, being lowest (subspecific at most) in the quasi-continental Balearics and continental Zanzibar and Mafia; and highest (a quarter of the species) in the oceanic islands of the Gulf of Guinea. In the Canaries, apart from some endemic species, subspecific endemism is high, partly in correlation with climatic differences within the archipelago.

Members commenting on points from this paper included Mr N. Wace, Dr N. M. Pritchard and Mr H. N. Southern.

The final contribution was by Dr. L. W. Poel on 'Quantitative studies of soil aeration using an oxygen diffusion meter'.

The paper was introduced by a brief survey of earlier methods of characterizing the oxygen factor in soil aeration. Many such methods suffered from the disadvantage that the sampling device was so large that micro-environments in the soil could not be resolved.

The oxygen diffusion meter, which was exhibited at the meeting, is a polarographic instrument employing a large saturated calomel reference electrode embedded at a convenient point in the soil surface and a stout platinum wire cathode inserted to the desired depth. The steady-state current obtained with a voltage of 0.8 volt applied across the electrodes is limited by the area of the platinum probe and the rate of diffusion of oxygen to its surface. Application of classical diffusion theory following certain assumptions enables values of current to be converted into weight of oxygen diffusing to unit surface in unit time.

Field data were presented for sites in the Wyre Forest. The highest values were encountered in well-drained Pteridietum, the lowest in waterlogged Juncetum conglomerati. Between these extremes, the data for various types of vegetation fell into a series, the order of which could be predicted from general observations of soils and vegetation.

Preliminary estimations at an upland pasture area in Perthshire lent support to the speaker's earlier conclusion that soil aeration is a factor determining the distribution of *Pteridium* and one involved in the competition between the fern and *Calluna*. The importance of estimating soil reaction at each site of oxygen diffusion estimation was stressed.

Unfortunately there was insufficient time to encourage discussion of this paper.

THE ANNUAL GENERAL MEETING

The 40th Annual General Meeting of the Society began at 10 a.m. on 3 January 1959. The following are the (unconfirmed) Minutes of this meeting.

MINUTES OF 40TH ANNUAL GENERAL MEETING

The President, Professor N. A. Burges, took the chair in the Lecture Theatre of the Department of Zoology and Comparative Anatomy, University of Oxford, at 10 a.m. on 3 January 1959.

(1) The Minutes of the 39th Annual General Meeting, having appeared in *J. Ecol.*, **46,** 3 and *J. Anim. Ecol.*, **27,** 2 were taken as read, and approved.

(2) The following Report of the Honorary Secretaries had been duplicated and distributed to members attending the meeting:

Report of the Honorary Secretaries for 1958

The 39th Annual General Meeting of the Society was held during the Winter Meeting in the Stern Hall, Queen Mary College, University of London, the chair being taken at 10 a.m. on 3 January 1958 by the President, Professor G. C. Varley. An account of the proceedings has appeared in *J. Ecol.*, **46,** 3 and *J. Anim. Ecol.*, **27,** 2.

Papers read at the Winter Meeting all concerned some aspect of the ecological significance of pH, base status and related factors. Those delivered on Friday afternoon, 3 January, by Dr O. J. W. Gilbert, Dr J. E. Satchell and Mr J. G. Blower, considered the activity and distribution of soil organisms in relation to these influences. Two papers the following morning, by Dr E. Gorham and Mr D. S. Tucker, related to the supply of certain ions in freshwater habitats and their influence upon vegetation and fauna. The concluding papers in the afternoon were devoted to aspects of the composition of peats as they concern the distribution and growth of certain plant and animal species, and were given by Dr D. J. Boatman, Mr A. J. P. Gore and Dr J. M. Boyd. On Friday evening an informal dinner was held in Queen Mary College, followed by a soirée in the

Departments of Botany and Zoology. The Society is most grateful for the invitation from the Principal to hold the meeting at Queen Mary College, and to Dr P. J. Wanstall for excellent local arrangements. Well over one hundred members attended the meeting.

The Spring Meeting was held at Bangor from 11 to 14 April when the Departments of Botany and Agricultural Botany were our hosts and the emphasis was on Land Use, and especially land use in hill country such as North Wales.

A soirée on the 11th was notable for the wealth and interest of its exhibits; further exhibits were on show in the Department of Agricultural Botany on the 14th. The papers read at the two morning sessions were as follows: Professor Dudley Stamp—'The mapping of land use'; Mr J. A. Taylor—'Growing season, its measurement and mapping'; Professor Alun Roberts—'Human settlement and land use in Snowdonia against the background of vegetation ecology in the area'; Dr R. E. Hughes—'The ecological approach to problems of land use in Snowdonia'; Professor W. H. Pearsall—'Land use and soil deterioration in Britain'; Mr J. M. B. Brown—'Ecological considerations in the use of waste land for afforestation'; and Dr D. N. McVean—'Position and prospects in Scotland'. Saturday afternoon was devoted to an excursion to Great Orme's Head or to a visit to the Marine Biological Station and a trip in the *Nautilus*. On Sunday half the members went to Newborough Warren and the other half were demonstrated the history of land use and sheep grazing in the Conway Valley and on Snowdon. The meeting was well attended and demonstrated Bangor as a centre of enthusiasts in pure and applied ecology; we are grateful to Professors Richards and Alun Roberts and Dr Hughes and Mr Greig-Smith for their hospitality and making the arrangements for this excellent meeting.

The Summer Meeting was held at Flatford Mill Field Centre and excursions were arranged to Dodnash Wood, the River Stour, Redgrave Fen, the Stour estuary and Horsey Island, the Suffolk villages, Staverton Thicks, Shingle Street and the Shellfish Research Laboratory at Burnham Crouch. A pleasant dinner was held in the evening of the 14th. The small attendance, while making the meeting pleasantly informal, did no justice to the excellent leadership and hospitality provided by Mr and Mrs Bingley and the Centre staff.

The Autumn Meeting planned for 19-22 September, which would have included various papers, excursions to industrial sites and Wyre Forest, unfortunately had to be cancelled owing to the small number of bookings.

Volume **46** of the *Journal of Ecology* was issued in three numbers. The first contained 216 pages, including an Obituary of Sir Arthur Tansley, 13 original papers, reviews of 8 books and 1 contribution to the Biological Flora; No. 2 had 319 pages and contained 12 original papers, 2 book reviews, reports of the Spring and Summer Meetings of the Society in 1957, the Balance Sheet and List of Members, a revised Schedule for Contributors to the Biological Flora and accounts of 2 species; No. 3 consisted of 248 pages containing 12 original papers, the account of the 1958 Winter Meeting and 9 book reviews. Besides the Notice to Contributors to the Biological Flora, Revised Schedule and list of Accounts in Preparation contained in *J. Ecol.*, **46**, 2, this volume included the following parts: *Daboecia cantabrica* K. Koch (S. R. J. Woodell); *Polemonium caeruleum* L. (C. D. Pigott) and *Viola lactea* Sm. (D. M. Moore).

The second part of Volume **26** of the *Journal of Animal Ecology* appeared early in the year. Part 1 of the current volume (**27**) contained 200 pages consisting of 11 original papers, reviews, abstracts, and the Society's accounts and proceedings. Part 2, published at the end of the year, contains 7 original papers, reviews, abstracts and the Society's membership list. It brings the pagination of Volume **27** up to a total of 464. The reprinting of Volumes **12** and **16** during the year makes complete sets of the Journal again available for sale. Non-member subscriptions have continued to increase and sales of back-numbers have been maintained at a high level.

The Council have met three times in the year to elect new members, plan future meetings and discuss the publication of the Journals and other activities of the Society. The Standing Committee on Publications has continued to deal with much of the detailed business connected with the Journals, and especially with the problem of the continued demand for publication space in the *Journal of Ecology* and the financial difficulties

involved in publishing a larger Journal. The Burren Committee was fully established in January and has made progress with its plans for investigations in the area. The Society has become a founder member of the 'Council for Nature' and our Council has taken a close interest in this new organization which may have considerable importance for ecology in Britain. The Council are arranging for the transfer to the Nature Conservancy of a collection of reprints and lantern slides, originally owned partly by the Society and partly by Sir Arthur Tansley. These collections will be accessible to members and others, and the transfer will end the past attempts of the Society to own a library without having any place to house it, and also leads logically to the Council's proposal to delete Rule 5b.

In October the Council appointed a new small Programme Planning Committee to advise it on plans for future meetings. The Committee has already recommended that in general there should be three meetings in the year; the Winter Meeting devoted mostly to papers on all aspects of ecology, the Summer Meeting of excursions concentrating on field ecology, and one symposium concentrating on an intensive coverage of one subject selected for its topical interest and fundamental importance. The Committee hopes that in this way the traditions of the Society's meetings may be maintained while at the same time being adapted to present-day conditions when scientific meetings are frequent and interests tend to be specialized. The first symposium on Weed Ecology is to be held in Oxford in April 1959.

The membership of the Society stands (at the end of 1958) at 1031. Owing to some further resignations following the increase in subscription (32 resignations were intimated during the year), 2 deaths and the loss of 17 members whose names were removed from the list owing to their subscriptions falling into arrear, this total does not represent much of an increase upon the previous year. However, the enrolment of new members continues at a very satisfactory rate (69 during 1958) and it seems likely that the steady rise in the Society's membership will be resumed in 1959. Members subscribing to both Journals number 168; those taking the *Journal of Ecology* only, 529; those taking the *Journal of Animal Ecology* only, 309. There are 2 Honorary Members, 6 Honorary Associates, and 17 Associate Members.

Finally, the Secretaries wish to thank all those who have given the Society hospitality during the year and those who have helped with the local organization of meetings. They are also grateful for the co-operation they have received from their fellow officers and the help given to them in secretarial assistance.

C. H. GIMINGHAM
E. D. LE CREN
December 1958 *Honorary Secretaries*

Dr C. H. Gimingham commented briefly on this report, which was adopted.

(3) Dr F. H. Whitehead presented the provisional report of the Honorary Treasurers. For the first time it had been possible, owing to prompt submission of accounts by the publishers, to present the completed accounts for the previous year, although these had not yet been audited. In a thorough analysis and comparison with 1957, Dr Whitehead showed that the Society's reserves were now very low, but that in 1958 the increased subscription rate had resulted in an excess of income over expenditure of £773. The report was approved.

(4) The deletion of Rule 5b from the Constitution and Rules, adopted on 6 January 1954, was proposed from the chair and unanimously agreed.

(5) The following, having been nominated by Council, were proposed from the chair and unanimously elected as Officers and Members of Council:

Vice-President: D. CHITTY
Hon. Secretaries: C. H. GIMINGHAM, E. D. LE CREN
Members of Council (to retire in 1963): F. FRASER DARLING, J. L. HARLEY, K. H. MANN, J. WARREN WILSON
(No other nominations had been received.)

(6) In his report as Honorary Editor of the *Journal of Ecology*, Professor P. W. Richards stated that the delay between receipt of a paper and its appearance in print had been reduced from a year or more to 8-10 months. However, owing to an influx of new papers he was doubtful if this position could be maintained. Following a recommendation by Council, it was hoped to encourage the submission of papers on experimental ecology to the *Journal of Ecology*, by giving priority to papers less than about ten pages in length.

In the absence of Mr H. C. Gilson no editorial report was presented for the *Journal of Animal Ecology*. Professor Richards's report was accepted, after considerable discussion, on the question of whether a strict upper limit should be set to the length of papers. It was felt by some speakers that under present circumstances this was necessary, but others, while agreeing on all measures to encourage brevity, felt that a rigid limit would have undesirable results.

(7) Reporting on behalf of the Honorary Editors of the Biological Flora, Dr D. E. Coombe mentioned that three parts had appeared in the past year, together with a revised list of Contributors and Schedule (see Secretaries' Report). He felt that the limits on length would have to be more strictly adhered to in future—although during the year these limits had been waived for the account of *Quercus* spp. Authors were urged to submit a draft of their accounts for editorial comment before preparing the final version.

(8) Two other items of business consisted of a summary of the programme for the forthcoming symposium on 'The Biology of Weeds' by Dr J. L. Harper; and a comment on the progress of the Burren Survey by Professor D. A. Webb.

Professor Burges drew the meeting to a close with an expression of thanks to Professor Sir Alister Hardy for the hospitality of his Department, Professor G. C. Varley for making the excellent local arrangements, and to the Treasurers and Secretaries of the Society.

C. H. G.

THE BRITISH ECOLOGICAL SOCIETY

Officers and Council for the Year 1959

President: N. A. BURGES *Vice-Presidents*: D. CHITTY, D. A. WEBB

Honorary Treasurers:

F. H. WHITEHEAD Department of Botany, South Parks Road, Oxford.

J. L. HARPER (receives subscriptions) Department of Agriculture, Parks Road, Oxford.

Honorary Secretaries:

C. H. GIMINGHAM (membership) Department of Botany, University of Aberdeen, Old Aberdeen.

E. D. LE CREN (Council) The Ferry House, Far Sawrey, Ambleside, Westmorland.

Honorary Editors of the Journal of Ecology: P. W. RICHARDS and D. E. COOMBE

Honorary Editor of the Journal of Animal Ecology: H. C. GILSON

Council (together with Officers as above):

Retiring: 1960	1961	1962	1963
P. F. HOLMES	D. J. CRISP	M. ASHBY	F. FRASER-DARLING
R. E. HUGHES	M. W. HOLDGATE	F. J. BINGLEY	J. L. HARLEY
T. T. MACAN	C. D. PIGOTT	P. GREIG-SMITH	K. H. MANN
F. E. ROUND	H. V. THOMSON	L. A. HARVEY	J. WARREN-WILSON

Honorary Editors of the Biological Flora:

A. R. CLAPHAM, D. E. COOMBE, C. D. PIGOTT, P. W. RICHARDS

The British Ecological Society was founded in April 1913, when it replaced the British Vegetation Committee (founded 1904). The object of the Society is to promote and foster the study of Ecology in its widest sense. This it does by publishing the *Journal of Ecology* and the *Journal of Animal Ecology*, and by holding regular meetings when papers are read and symposia and discussions on subjects of current ecological interest are held. At present these meetings are held in early January, March or April, and September, in London, Oxford or Cambridge or a provincial centre. A fourth meeting in July is devoted primarily to field excursions from a convenient centre to places of ecological interest.

MEMBERSHIP of the Society is open to all, whether or not they reside in the British Isles, who are genuinely and personally interested in Ecology and wish to receive the Society's journals for their own use. The minimum subscription for membership is 40*s*., due on January 1st each year. This entitles members to receive *one* of the two journals, to attend the meetings and make use of other facilities that the Society may offer, to vote in the election of Council and Officers and be eligible for election to Council and Office. For a subscription of 70*s*. members may receive *both* journals. Membership does not include the right to any reduction in the price of back numbers of the journals, except those published in the year of election.

ASSOCIATE MEMBERSHIP of the Society is open to those who wish only to attend meetings. Associates pay an annual subscription of 7*s*. 6*d*. and do not have the right to receive a journal or vote at a meeting of the Society.

Local Natural History Societies, Field Clubs and other similar bodies are eligible for a special membership of the Society.

Full details of membership and an application form may be obtained on request from either of the Honorary Secretaries.

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CONTENTS

PAGE

Notice to Contributors ii

C. K. Capstick. The distribution of free-living nematodes in relation to salinity in the midde and upper reaches of the River Blyth estuary 189

R. O. Brinkhurst. Alary polymorphism in the Gerroidea (Hemiptera-Heteroptera) 211

R. D. Hughes and Dorothy D. Salter. Natural mortality of *Erioischia brassicae* (Bouché) (Diptera, Anthomyiidae) during the immature stages of the first generation 231

S. Markowski. The cooling water of power stations: a new factor in the environment of marine and freshwater invertebrates 243

A. F. G. Dixon. An experimental study of the searching behaviour of the predatory coccinellid beetle *Adalia decempunctata* (L.) 259

J. S. Alabaster. The effect of a sewage effluent on the distribution of dissolved oxygen and fish in a stream 283

T. H. MacDonald. Estimates of length of larval life in three species of lamprey found in Britain 293

E. W. Bentley. The distribution and status of *Rattus rattus* L. in the United Kingdom in 1951 and 1956 299

G. Williams. Seasonal and diurnal activity of Carabidae, with particular reference to *Nebria, Notiophilus* and *Feronia* 309

J. A. Kitching, J. F. Sloane and F. J. Ebling. The ecology of Lough Ine. VIII. Mussels and their predators 331

R. D. Hughes. The natural mortality of *Erioischia brassicae* (Bouché) (Diptera, Anthomyiidae) during the egg stage of the first generation 343

R. J. A. W. Lever. The diet of the fox since myxomatosis 359

T. Lewis and J. W. Siddorn. A simple portable recorder for direction and speed of wind 377

Reviews 381

Books Received 393

Abstracts 395

British Ecological Society
Winter and Annual General Meeting 411

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